ECOLOGY

VOL. 33 OCTOBER, 1952 No. 4

EXPERIMENTAL METHODS IN POPULATION DYNAMICS: A CRITIQUE

FREDERICK E. SMITH
Department of Zoology, University of Michigan, Ann Arbor, Michigan

INTRODUCTION

Until very recently, deterministic theory has been the source of mathematical models for population dynamics. Simple equations have been proposed as suitable representations of sigmoid growth, competition, predation, etc., and these have been fitted to various data. The studies of Gause (1934) epitomize this field.

Stochastic theory provides a kind of model that expresses, not only the general sequence of events, but also the inherent variability of the system. While the deterministic function may represent the "pure" curve of maximum likelihood, the stochastic function permits an evaluation of the actual, observed curve, regardless of its irregularities. Since this ability to handle chance variations and their sequential effects during dynamic processes is relatively new, one must conclude that its future effect upon the approach to population dynamics will be one of progressive increase.

As the theoretical approach is shifting its base, it would be well to look closely to the experimental methods that are in use. The intent of such a critique is two-fold: to determine what has actually been accomplished by such methods, as opposed to what is supposed to have been accomplished, and to launch the newer theoretical approach upon a somewhat better methodology.

Only a few aspects of the experimental techniques are discussed, serving to emphasize phenomena that may well be extended to other aspects. Those discussed fall into the following sections: the mechanisms of culture, the responses of the population, certain properties of deterministic theories, and the application of theories to data. It is the methods that are criticized; such criticisms as occur on the usefulness of particular theories are more or less incidental.

While this paper represents the views of one individual, its existence is very much a result of discussions with E. S. Deevey, G. A. Riley, L. B. Slobodkin, D. W. Calhoun, and especially with G. E. Hutchinson, all at Yale University. Later developments reflect the influence of many others in several places.

THE EXPERIMENTAL ENVIRONMENT

Experiments in population dynamics are accomplished in cultures, and associated with these cultures are specific environments. One advantage of an experiment over field studies is the possibility of simplifying the environment through appropriate manipulation of the culture.

The culture can be treated in many ways, producing various qualitative effects in the environment and hence upon the population. If the experiment is designed as a test of some theory, the manipulations should be such as to simulate the conditions implied by the theory. Thus, if one were to test the

predation theory of Lotka (1925) and Volterra (1928), the environment would have to be such that the growth of the prey were in no way inhibited by prey density.

Surprisingly little attention has been paid to the possibility that a given theory, under investigation, defines certain properties for the experiment. In an attempt to emphasize such relationships, a very crude system of classification is given for several culture techniques that may be used in the laboratory. To these will be related the corresponding environments, and the latter will be associated with particular theories.

From the standpoint of ease of interpretation, the simplest culture technique is the *unlimited* culture. Either the population is continually so rarefied or the culture is so rapidly enriched that the organisms never suffer any inhibitive effects upon each other, at least not during the course of study.

Among culture techniques that have limited capacities for growth, the *unrenewed* culture is most frequently used, especially in bacteriology and protozoology. The culture is innoculated, and the subsequent history of the population is recorded. Nothing is added or subtracted by the experimenter.

A variant of this technique is the *periodically renewed* culture. At regular intervals, either the entire population is transferred to a new culture (as is done with flour beetles) or the culture is given booster shots of concentrated medium (as has been done with protozoa).

A still further refinement is the *continuously renewed* culture. The intervals between renewals are so small as to be ineffective, and the system can be treated as though fresh medium is being flushed through at a constant rate all of the time.

While these are but a few techniques, they are simple, and adequate for the present purpose.

Associated with each culture, and determined by the particular factors that are limiting, is a corresponding environment. In the unlimited culture, of course, since nothing is limiting, the environment is of the same type, an unlimited environment.

If the limiting factor is an expendable component of the medium, such as sugar or amino acid, the environment will follow the pattern of the culture.

If the limiting factor is non-expendable, such as space, the environment will in all cases follow the continuously renewed pattern, since the factor is resupplied automatically by the death of individuals. If spatial organization is involved, however, the rhythmic disturbance of the periodically renewed environment may produce a significant effect.

If the limiting factor is a freely diffusable substance like oxygen or carbon dioxide, again the system will in all cases regulate toward the continuously renewed pattern.

If the limiting factor is a noxious metabolite, the environment will follow the pattern of the culture, except that adding booster shots accomplishes little, and this type of culture will be modified toward the unrenewed type.

While these are but a few possibilities, they are enough to indicate some patterns that may occur. Combinations of limiting factors will complicate these patterns, so that, for example, it is not unlikely for an unrenewed culture to be temporarily regulated toward a continuously renewed environment by the supply of oxygen, only to revert to type later as the food is exhausted.

If we now examine some of the published theories, the implied environmental types (extrinsic to the interspecies relation when two populations are involved) are as follows:

1. Unlimited environment: exponential growth (Malthus 1798), predation (Lotka 1925; Volterra 1928), and the host-parasite relation

(Nicholson and Bailey 1935; Thompson 1939).
2. Unrenewed environment: sigmoid growth (Klem 1933).
3. Periodically renewed environment: none.
4. Continuously renewed environment: sigmoid growth (Verhulst 1838; Pearl and Reed 1920; Gompertz and Wilson, both in Wilson 1934) and indirect competition (Volterra 1928; Gause 1934).

In experiments on exponential growth, the culture has usually been so manipulated as to provide the proper environment. This is not known to be so for any of the experiments on predation; in those of Gause (1934, 1935) and of Gause, Smaragdova, and Witt (1936) the prey definitely reached densities that inhibited their own rate of growth. The same is true for most of the experiments on the host-parasite relation. Only one, an experiment by DeBach and Smith (1947), specifically eliminated self-inhibition in the growth of the prey population.

Klem's theory of sigmoid growth was developed for his experiments on yeast. The event appears to be unique, since no one else has applied a theory of growth in an unrenewed environment to data from an unrenewed environment.

While no theories have been developed to include the rhythmic effects of periodic renewal, many experiments have been recorded in which such effects probably existed. This would apply especially to studies of flour insects.

No ecological experiment has been conducted in a continuously renewed culture, although such techniques can be adapted from the work of Novick and Szilard (1950) or of Myers and Clark (1944). No experimental environment has ever been proved to be continuously renewed. While the chances are very good that in some experiments the unrenewed or periodically renewed culture technique that was used was modified by the limiting factors toward a continuously renewed type, this cannot be said with assurance for any particular case.

In summary, from the point of view that an experiment should simulate the conditions of the theory to which it is compared, very few of the published comparisons are known to be suitable. It is known for only one experiment on sigmoid growth (in which the theory did not fit the data well), one experiment on the host-parasite relation (in which the fit of theory to data is fair), and for many experiments on exponential growth. All of the remaining comparisons are open to question.

The Experimental Population

While theories developed in population dynamics are admittedly oversimplified, a general awareness of this in experimental terms seems to be deficient. For, again, if the data are to be used as a "test" of a theory, they should be derived from an appropriate ecological system.

An almost universal simplification in theories is that the unit of the population, the organism, always bears the same relation to the environment. While this is never true, if the distribution of (qualitative) variations among the units is always similar, the approximation is satisfactory.

But stability or constancy of such properties as size-distribution, age-distribution, sex-ratio, etc. is surprisingly rare. Even in the most simple case of population dynamics, exponential growth, marked changes in the population during a recorded phase of such growth are frequent. Demonstrations of such changes are relatively infrequent, since more than one measure of the population has to be taken if a change is to be discerned.

Hershey (1938) demonstrated that, during the period that the cell count was increasing along a good exponential curve, the rate of nitrogen uptake in the

population was increasing along a different curve, having a rate function at least 30% smaller. Obviously some character of the population was changing with time; the organism did not stay the same.

The most striking demonstration of this phenomenon was found by Richards (1932) in yeast. During the thirty hours of exponential increase in cell count, the percentage of budding cells increased steadily from 10 to 25, the percentage of moribund cells fell exponentially from 7 to 1, and the surface-volume ratio increased from about 2.9 to 3.4. Richards remarked that the sigmoid growth of yeast was too complicated for comparison to "formulae with arbitrary constants which over simplify the various influences that determine the extent of natural unlimited growth of the cells"; this remark applies equally well to the exponential phase of growth.

Finally, it is a commonplace in bacteriology that cell-count curves and colorimetric curves do not agree.

The conclusion from these demonstrations is that, although the culture is mechanically of the proper type, insufficient time is allowed for the population to adjust to exponential growth. Before the population is able to "settle down," it becomes crowded and passes into plateau. This may be avoided (Hershey 1939) by subculturing from very young cultures. Effectively the period of exponential growth is prolonged, and a steady state of population characteristics is able to develop. In an adjusted culture, all estimates of the growth rate (number, total volume, nitrogen uptake, etc.) must be the same. Most of the published observations of exponential growth are probably inaccurate estimates of the "true" rate of increase.

The concept of unchanging population characteristics in sigmoid growth or in other ecological relations is absurd. This has been recognised, and such "simple" organisms as yeast, protozoa, and bacteria have been used with the assumption that, here, at least, qualitative changes are minimal. It would now appear that such an assumption is unwarranted. The reactions of yeast to environmental stress, as recorded by Richards (1932), are fully as complicated from a mathematical point of view as those of any higher organism.

It is unfortunate that just those species which culture easily (yeast, flour insects, fruit flies, etc.) come from naturally unstable environments. Their complex adaptabilities, which facilitate culture, are precisely what complicate the population experiment. A simpler system would be one using species (not necessarily simple) from stable, uniform environments—species that usually are difficult to culture. Another possible solution is to present the traditional laboratory species with totally new limiting factors, and gamble that the population response will be relatively simple.

It is possible that in some experiments physiological adaptation to stress has combined with an unsuitable environmental type to produce a deceptive result. This is especially likely in comparisons of sigmoid growth with the Verhulst-Pearl theory. In many yeasts and bacteria, as growth proceeds in the unrenewed culture, the population shifts progressively to an inactive state. In an unrenewed environment one would expect the upper part of the sigmoid curve to be small, since it is curtailed by a falling capacity in the culture. After the peak of growth the population, if it could not adapt, would fall, perhaps along a negative exponential. But in these cases, the sum of inactive and active cells enlarges the upper portion of the growth curve and postpones the fall almost indefinitely.

While the result may be described closely by the mathematical form of the Verhulst-Pearl logistic, such a description is not useful. Either the combination of two errors has produced a

fortuitous result, or their interaction is regulated by a process as yet unsuspected. In either case the theory does not describe the underlying biology.

Other complications that may be introduced by the organisms cannot be treated lightly. These include environmental conditioning, changes in the age structure of the population, and mutation with a complete replacement of the population (as occurs frequently in the chemostat of Novick and Szilard 1950). Whatever the specific complications, they must be reconciled in any comparison of theory and experiment.

Properties of Deterministic Theories

Any equation in population dynamics has specific properties, properties which are obvious to the mathematician, but which seem to have escaped any degree of experimental application. Many of these properties are useful, in that some of them may show immediately that the theory has limitations, while others may provide tools for study. These properties will be discussed by examples.

The theory of Verhulst (1838) and Pearl and Reed (1920) has the following form:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

where N = population size,

t = time,
r = intrinsic (net, maximum, exponential) rate of increase,
K = saturation level or plateau,

expressing the rate of change of the population (dN) with respect to change in time (dt). The equation can also be written as the average rate of change for the individual (dN/N) with respect to the change in time:

$$\frac{dN}{Ndt} = r\left(1 - \frac{N}{K}\right).$$

In this latter form, the average growth rate is seen to be a linear function of the degree of saturation (N/K). Thus, when this ratio is nearly zero, the growth rate is maximal (r), when it is one-half, the growth rate is one-half, and when the system is just saturated, the growth rate is zero.

In unrenewed environments, and in competitive and predative relationships, the possibility of a population level exceeding the current saturation level must be considered. In the Verhulst-Pearl theory, the linear relation continues; when the system is twice saturated, the growth rate is minus r, when it is ten times saturated, the rate is minus $9r$. Thus, the rate of decrease is not a limited function. Lotka (1925) indicated that this property may not be suitable for some situations.

The Verhulst-Pearl theory stands up under this kind of analysis better than most. In the Gompertz theory (Wilson 1934), the equation can be stated:

$$\frac{dN}{dt} = rN \log_e\left(\frac{K}{N}\right)$$

or:

$$\frac{dN}{Ndt} = r \log_e\left(\frac{K}{N}\right).$$

This equation has the same limitation as the Verhulst-Pearl theory, setting no limit to the rate of decrease. It has the more serious fault, however, of setting no limit to the rate of increase. When the ratio, N/K, is small, the rate of growth approaches infinity. It is only between about one-third saturation (where $\log_e K/N$ is 1.0) and full saturation (where $\log_e K/N$ is 0.0) that the constants of the equation can be interpreted biologically.

As a final example, the predation equations of Lotka (1925) and Volterra (1928) are:

$$\frac{dN_1}{dt} = r_1N_1 - k_1N_1N_2$$

$$\frac{dN_2}{dt} = k_2N_1N_2 - d_2N_2$$

where N_1 = prey population,
N_2 = predator population,
r_1 = intrinsic rate of increase for the prey,
d_2 = exponential death rate of the predators,
k_1,k_2 = predation constants.

If the predation constants are taken as simple, as they were in the development of an intrinsic cyclic relation, some of the properties are as follows:

$$\frac{dN_1}{N_1dt} = r_1 - k_1N_2,$$

$$\frac{dN_2}{N_2dt} = k_2N_1 - d_2.$$

1. Neither species enters in its own average growth function; hence, neither ever inhibits its own growth; the environment extrinsic to the relation is unlimited.
2. Prey density has no effect upon the likelihood of a prey being eaten; there is no safety in numbers.
3. Predator density has no effect upon the likelihood of a predator catching a prey; there is no competition for food.
4. The predators have an unlimited rate of increase.

While (1) can be arranged mechanically, and (2) may be true if the predators are certain filter-feeders, (3) and especially (4) are biologically unknown. These simple interpretations of the predation constants must be considered useless. To do so at once invalidates the predation "laws" of Volterra and the regular intrinsic cyclic relation developed by both Lotka and Volterra.

A more complex interpretation of the predation constants is that:

$$k_1 = a + bN_1 + cN_2 + \ldots$$

$$k_2 = a' + b'N_1 + c'N_2 + \ldots$$

defining each as a power series (Lotka 1925). If we consider only the second function, k_2, it is evident that a power series is most inept for its purpose.

For the growth function of the predators to be satisfactory, the average rate of growth (dN_2/N_2dt) must rise to some asymptote (r_2) as the prey are made more numerous. To describe such a curve by a power series that will handle all values of prey up to infinity, an infinite number of terms and constants are needed. Even to handle the numbers of prey that are likely to develop in an experiment requires several terms of the series. Furthermore, the function fails markedly should the prey density exceed that expected and allowed for. The use of exponential functions, as suggested by Gause (1934), offers a much higher efficiency in terms of the number of constants that would be required to describe this relation.

So far in this section only the deficiencies of theories have been emphasized. The second use of such an analysis of equations is to develop experimental tools. These will be discussed at the end of the following section.

The Application of Theories to Data

Actually, little can be said in favor of the fitting of deterministic theoretical curves to empirical data. The technique, as a means of "testing" theories, is indefensible on at least three independent counts:

(1) Judgment has to be subjective. Deviations from the best-fit curve always occur, and statistical methods for evaluating these deviations are lacking.

(2) The prior probability of the method is high. This aspect of probability is too often ignored; regardless of the calculated probability of a particular fit, if it is likely to be good before the fit is made, the test itself is inefficient. The method is uncritical; while it may exclude extreme misfits, it fails to discriminate among a host of similar but basically different situations.

Kavanagh and Richards (1934), among others, demonstrated that a variety of theoretical curves could be fitted to the same data on sigmoid growth, and with equal felicity. An even more powerful criticism of this weak method is the fact that the theory of Verhulst and Pearl, for example, has been accepted as a satisfactory fit to a remarkably heterogeneous set of ecological situations. The heterogeneity emphasizes, not the generality of the theory, as is usually assumed, but the weak method of application. The problems discussed in the preceeding sections have not caused difficulty in the past because the established method of fitting theories is not powerful enough to discriminate them.

This weakness is related to the number of constants fitted in the process of comparing a curve to data. With more than two such constants, the prior probability of a "nice" fit (a subjective term to match the subjective basis of judgment) is already high, and with more than four constants to be fitted to one population curve it is hardly necessary to make the comparison.

(3) The method centers attention on the whole rather than on the parts. A direct result has been a general satisfaction with the wholes, without the realization that at least some of the parts in the comparison are not of the right kind. If the overall fit is "nice," a prejudice is established against a rejection of the comparison through some particular fault.

The best fit of a theory to data has been said to be that of the Verhulst-Pearl theory to the growth curve of a yeast culture (Allee *et al.* 1949). The data were gathered by Carlson (1913), and the fit was made by Pearl (1930). In spite of this belief, the culture was unrenewed, the limiting factors were probably at first the food supply (sugar) and the waste accumulation, shifting later to the lower usefulness of the wastes as foods and the re-use of material from burst cells; the culture ended by converting to resting cells!

These three arguments are an unfortunate combination. A high prior probability leaves one at a loss in subjective judgement; the usual standards are not adequately strict. The lack of objective evaluation in whole comparisons, which has been accepted as a necessary evil, has forestalled any degree of partial analysis, in which objective methods are indeed possible. The lack of partial analyses has in turn promoted the habit of fitting all constants, whether some can be calculated independently or not, thus pushing the prior probability to its maximum.

For the comparison of whole theories to the history of a culture, the developing field of stochastic processes offers the only reasonable approach.

But whole comparisons may not be the best way to test theories. The danger still remains that the whole need not be the sum of the right parts. Rigorous testing of the separate aspects of the theories would not only simplify the mathematics, but would eliminate, at least to some degree, this last criticism.

In the Verhulst-Pearl theory, two basic concepts are combined. One is that the exponential rate of growth has a maximum (r), and the other is that the degree of saturation (N/K) is a linear depressant of the rate of growth (dN/Ndt).

The first concept is well supported and established. To measure it in a particular case, however, may be difficult. If there is to be any assurance of its accuracy it should be obtained from at least two kinds of measures in the growing population. Such estimates can be made "deterministic," in the sense that the average of many observations of a constant will approach its deterministic value. Furthermore, the empirical range of error would, with a suitable distribution, provide a means of probability evaluation. The two measures

can be tested for the absence of trend and for agreement with each other.

The second concept has never been analysed. Rate curves derived from growth curves are not adequate, since they contain the same stochastic processes as the original data. But the problem can be handled in a different way. In the equation:

$$\frac{dN}{Ndt} = r\left(1 - \frac{N}{K}\right) = r - \frac{r}{K}(\mathrm{N})$$

a graph of the rate of change (dN/Ndt) plotted against the population size (N) shows a straight line, with a y-intercept of r, and x-intercept of K, and a slope of $-r/K$.

Points for this graph could be obtained from a modified chemostat. Keeping the composition of the inflow constant, its rate (the washing-out rate, V/W) can be set at various levels between r and zero. At r, the system will be unstable, but for any rate of flow less than this the population will increase until its growth rate is density-depressed to the rate of flow ($dN/Ndt = V/W$). At each level of this flow, after the system comes to a steady state, a series of observations can be made on the population size (N). The data can then be put through the standard statistical test (again, if a suitable distribution is found) to determine whether the regression of population size (N) upon the rate of growth (dN/Ndt) is linear. This would be a first test of the basic principle of the theory.

Needless to say, this method will apply to other theories of sigmoid growth. In the Gompertz curve, the linear plot becomes:

$$\frac{dN}{Ndt} = r \log_e K - r \log_e N.$$

The procedure can be turned about, to use the methods of partial analysis as a means of finding simple functions for theories. If, for example, none of the functions in established theories worked, a search with the aid of these partial systems may produce suitable relationships. Any experimental technique which will produce a steady state should yield information that can be used in deterministic theory.

The Lotka-Volterra predation theory indicates that:

1. A plot of dN_1/N_1dt against N_2 is a straight line, with a y-intercept of r_1 and a slope of $-1/k_1$.
2. A plot of dN_2/N_2dt against N_1 is a straight line, with a y-intercept of $-d_2$ and a slope of $1/k_2$.
3. dN_1/N_1dt, for one value of N_2, is constant for all values of N_1.
4. dN_2/N_2dt, for one value of N_1, is constant for all values of N_2.

Even these partial analyses, however, are not foolproof. Straight lines are easier to obtain than most people believe. If the data conform to a straight line "except at one end," or if they conform to two straight lines with a "break" in the middle, a linear relation is probably absent. Furthermore, small deviations toward one end of a curve may reflect large discrepancies in the dynamic processes of growth. For the faith that is put into population theories, the experimental examination will have to be rigorous.

Discussion

The preceding sections point to one conclusion: very little in this field of population dynamics is beyond the hypothetical stage. With the possible exception of the concept of exponential growth, it is a misuse of terms to refer to any of the interpretations as "theories." Almost all of the evidence used in support of various interpretations is, at best, inconclusive.

Yet, the field has provided a considerable fund of interesting material, enough to have profound effects upon allied areas. Perhaps, more than anything else, this influence urges an intense and cautious re-examination of our concepts.

The degree of acceptance of such concepts as, for examples, the Verhulst-Pearl logistic and the Lotka-Volterra equations, is astonishing.

Concepts do not appear easily. Although logic teaches that an infinite number of curves can be fitted to data on sigmoid growth, very few such equations have been set down, and of these only two, the Verhulst-Pearl and the Klem equations, have been expressed adequately in ecological terms. We have only one well-known theory of predation, one of competition, and two or three for parasitism. Sparse as it may be, this collection is the accumulated work of many people for many years.

Hence, even though the present stock of concepts is but a collection of hypotheses, it is a valuable collection. It contains what must be considered progress of the most difficult kind. For the future, also, the continued development of hypothetical relationships will be useful; the armchair is still a necessary piece of equipment.

The experimental side of population dynamics is in a different situation. In spite of the many curves recorded, the many fits made, the work will have to be largely discounted as evidence in support of any particular theories. A repetition of all of it, with more appropriate and more carefully detailed designs, will have to be initiated.

Regardless of the use to be made of stochastic processes, deterministic theory will continue to play a major role. It is a way of thinking; inevitably one considers, not the sequential range of values, but the most likely course of events. Most important, thinking in deterministic terms is a way of producing concepts.

Summary

The methods for experimental verification of deterministic theories in population dynamics are criticized from several points of view.

The mechanism of control in the culture should conform to the conditions implied in the theory. This is often not the case; the most notable instance of disagreement concerns the Verhulst-Pearl logistic, which has never been supported by an experiment known to be made in an appropriate environment. Several kinds of culture control are classified.

The reactions of the population should be limited to those provided in the theory. Most equations are admittedly simplified, but such an admission should be coupled with a much more successful restriction to simplified responses by the organisms. Many laboratory species are highly complex in their reactions to environmental control; physiological adaptation is especially common. A simple response is probably unrelated to evolutionary complexity. Two possible means of finding ideally simple reactions are indicated.

Theoretical equations are manipulated to show various of their properties. The method is useful as a means of "*a priori*" evaluation of equations, especially of their limitations. It is also useful as a means of discovering more simple but vital aspects of theories for specific analysis.

The common method of fitting deterministic curves to data is criticized from three points of view, any one of which raises a serious objection. One solution to the problem in the use of stochastic theory is mentioned, but methods are also discussed for the application of sound experimental techniques to deterministic theory.

The general conclusion is that we have a useful and valuable stockpile of concepts, but that up to the present little of the experimental work is at all conclusive. Most of the ideas in this field should be regarded as hypotheses, not theories.

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ENVIRONMENT AND FOREST DISTRIBUTION OF THE PALOUSE RANGE IN NORTHERN IDAHO

JOHNSON PARKER

University of Idaho, Moscow, Idaho

INTRODUCTION

Moscow Mountain and the immediately adjacent hills, known as the Thatuna or Palouse Range, occupy a position between the heavily forested mountains of northeastern Idaho and the plains of eastern Washington and nearby Idaho. Coniferous trees largely dominate the range (Fig. 1) but some half-dozen species are well enough represented and of similar enough requirements so that the distribution seems quite complex. Closer examination of the area, however, shows transitions from one species or group of species to another as the topography changes in certain respects.

Ecologists have already studied the distribution of these conifers in similar forests of northern Idaho and have provided various explanations for this distribution (Weaver 1914; Larsen 1929, 1930, 1940; Huberman 1935; Daubenmire 1942, 1943, 1946; Larrison 1946). However, little sociological work has been done in northern Idaho and practically no use has been made of the transect system described in this paper. Also the environment of the Palouse Range, in

FIG. 1. View from Route 95 looking northeast toward the Palouse Range. Paradise Point is at the left, West Twin and East Twin in the center, and Moscow Mt. at the right. The white zone at higher elevations is an ice deposit on the trees.

spite of its accessibility and the relatively uncut condition of the forests, has been only slightly studied.

In an attempt to clarify further the transitional changes in vegetation in a rather typical northern Idaho forest, to gain a clearer idea of the distribution of trees of the Palouse Range for purposes of comparison to other areas, and to study the environmental causes of this distribution the following work was carried out.

Methods

In order to study the forest transitions, the plot transect method was used. A plot was laid out 10 meters on a side and each species tallied for each of three diameter classes: 2–6 in., 6–10 in., and 10 in. and over d.b.h. The next plot was laid out directly adjacent to the first, the next adjacent to this, and so on along a compass line.

In order to determine how typical the Palouse Range was of the surrounding area, a mapping study was made according to certain vegetational groups (Fig. 2). Boundaries are often rather arbitrary because of cutting, burning, or cultivation but are given as closely as possible for this rough method of survey.

Comparisons of the microclimate on north and south slopes of the various hills of the range were made with the usual instruments. The temperature of the air three inches over the ground was recorded on each of two thermographs.

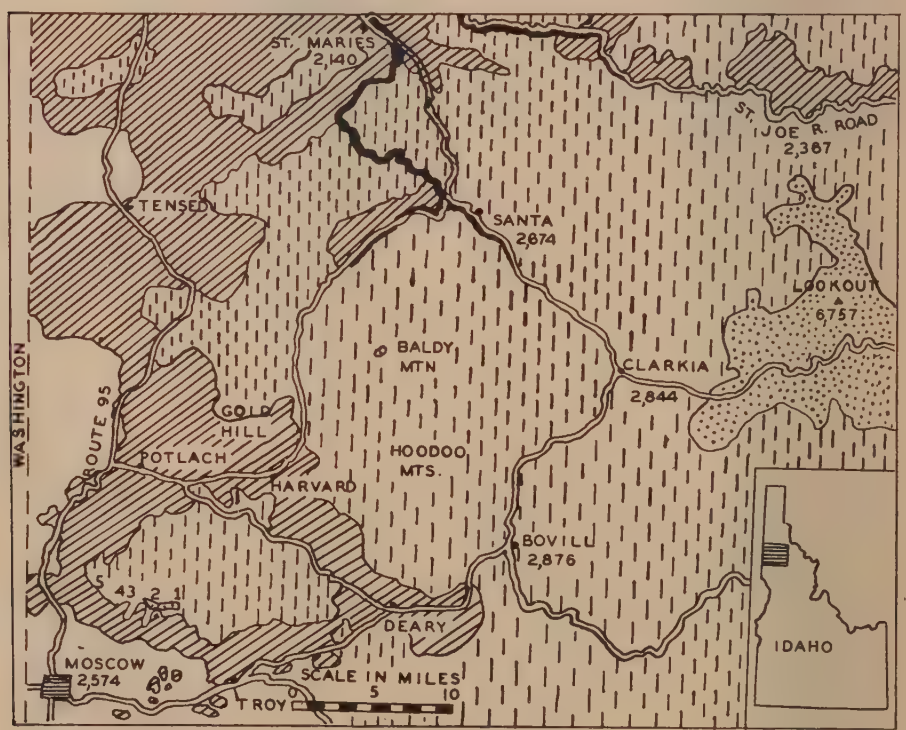

Fig. 2. Map of area near Moscow Mt. showing principal roads and forest types. Stippled: *Picea engelmanni* with or without other species; vertical dashes: *Pinus monticola, Larix occidentalis, Thuja plicata, Abies grandis, Pseudotsuga taxifolia;* cross hatching: *Pinus ponderosa* with or without *Pseudotsuga* or *Pinus contorta* with or without these other two; blank: grassland; black: riparian. Numbers refer to parts of the Palouse Range: 1, East Moscow Mt., 2, Moscow Mt., 3, East Twin, 4, West Twin, 5, Paradise Point.

TABLE I. *Habitat groups of the Palouse Range are shown horizontally and the species occurring in these groups are shown vertically. (C = climax species; S = successional species; small letters are used to denote low abundance, capitals to denote high abundance)*

Habitat group	Species							
	Picea engel.	*Thuja plicata*	*Larix occid.*	*Abies grandis*	*Pinus monticola*	*Pseudo-tsuga*	*Pinus ponderosa*	
Picea engelmanni	C			S?			s	moist soils
Thuja plicata		C	s	S	S	s	s	
Abies grandis			S	C	S	S	s	interm. soils
Pseudotsuga						C	S	
Pinus ponderosa							C	dry soils

Soil temperatures were obtained with an ordinary glass thermometer. Wind velocity was measured on the north and south slopes simultaneously by means of two standard type four-cup anemometers. A sling psychrometer was used to measure relative humidity. Maximum and minimum temperatures of the air six feet over the ground were obtained with a Six-type thermometer set out at each of three elevations as indicated in Table II. Each thermometer was fixed to the north side of a tree and read and reset at the end of each month. The thermometers were calibrated against a Weather Bureau-type maximum and minimum set of thermometers.

Soil samples from different slopes as indicated in Table III were obtained with a soil auger. Samples were placed in aluminum containers, taken to the laboratory, and measured for total moisture by the usual oven-drying gravimetric method. Xylene and moisture equivalents were made by the centrifuge method after sieving through a 2 mm. sieve.

RESULTS

Tree distribution

A number of zonational systems have been proposed by various writers as pointed out by Daubenmire (1946) and all of these systems seem to place the forests into three general zonal groups for the northern Rocky Mountains. These three groups, including Hudsonian, Canadian, and (forest) Transition, or according to another system, Subalpine, Upper Montane, and Lower Montane, are found in the Palouse Range (Fig. 2). Since much of the forest on this range fits into the Upper Montane zone further breakdown is often tempting. A more detailed system has been worked out by Daubenmire (1952) which is the basis of Table I. This system has the advantage of indicating the future successional trends in each habitat group. However, there are some ecologists who are not interested in long term successional trends and find the system too detailed for practical use.

While the controversy over different zonational systems continues unabated, it is apparent that any system which puts large populations of different plants into strict categories meets with certain difficulties in the field. The reason for this difficulty can be seen by examining the transects shown graphically in Figures 3 through 6. There are places in the Palouse Range where fairly sharp vegetational changes occur and these can be called ecotones (Figs. 5 and 6). It is more common, however, to find transitions between different concentrations of one species or a number of species in different areas, as, for instance, in gulches (Fig. 4) and even on hill crests such as the foothills of West Twin (Fig. 3). This sort of situ-

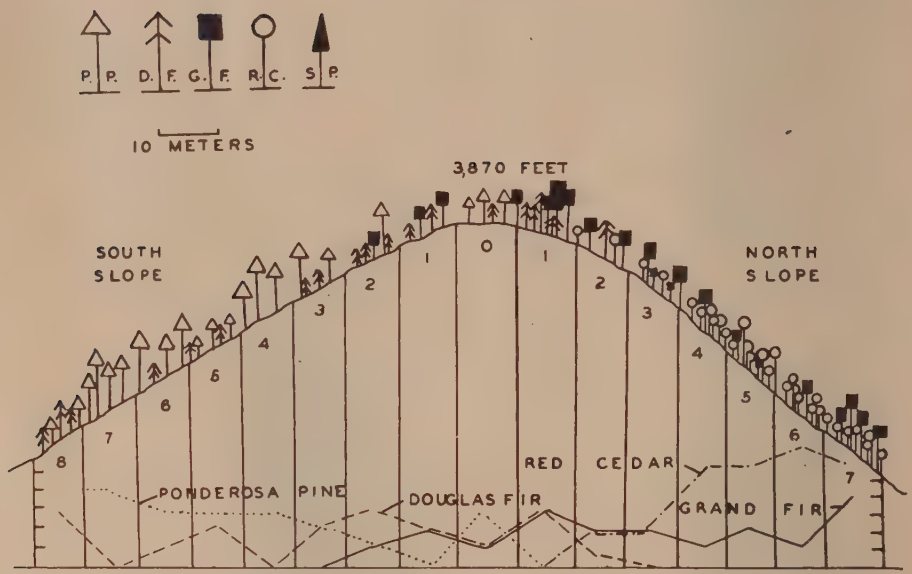

FIG. 3. Cross section of Gnat Hill near West Twin. P.P.: *Pinus ponderosa*, D.F.: *Pseudotsuga*, G.F.: *Abies grandis*, R.C.: *Thuja plicata*, and S.P.: *Picea engelmanni*. Numbers of trees for each 10 meter wide quadrat are drawn and also given graphically below.

ation, pointed out by Whittaker (1951) for certain eastern forests, appears to be the rule rather than the exception. There is seldom a pure stand on the north slopes of the Palouse Range; in any 100-square meter area there may be a mixture of two or three species. As one progresses away from this plot up or down the slope one

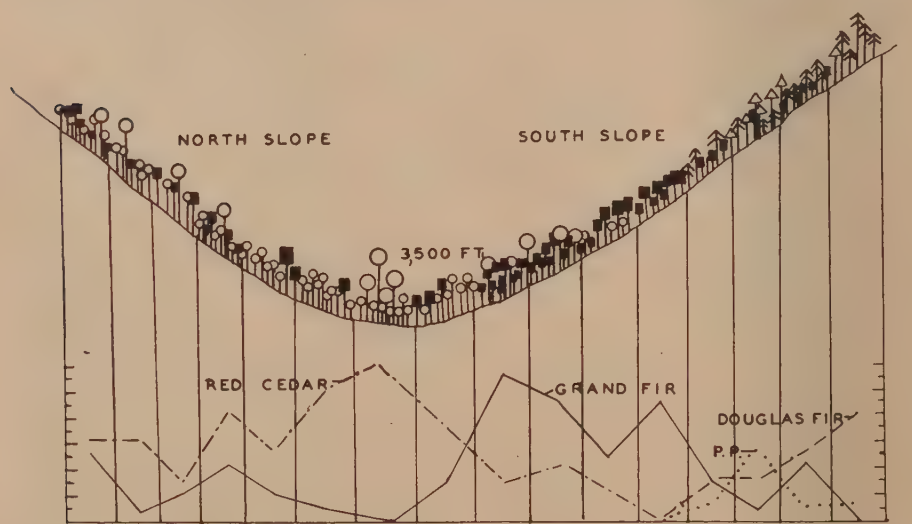

FIG. 4. Gulch below Gnat Hill at left and approach to West Twin at right. Same symbols as in Figure 3.

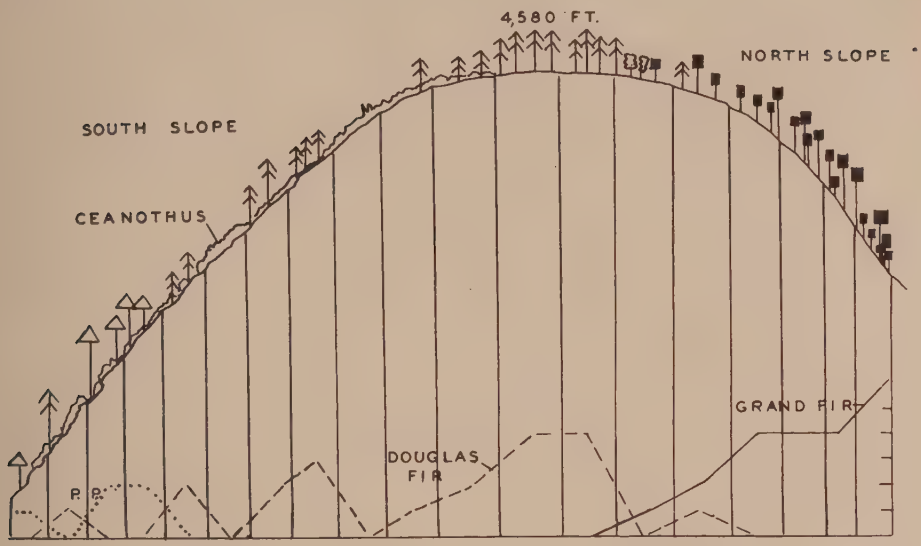

FIG. 5. Top of West Twin. Same symbols as in Figure 3.

species may decrease while another may increase.

Such transitional changes can also be demonstrated by the transect method in the *Picea engelmanni–Abies grandis*[1] stands near the top of Moscow Mountain. With increase in altitude, *Thuja plicata* tends to drop out but it is again difficult, although possible to draw a definite altitudinal line for its upper limit.

Looking at the mountain range as a whole, there is usually an *Abies grandis–Thuja plicata* mixture on north slopes with more *Thuja* in the moister areas than *Abies*. Extensive areas of the north slopes have been cut and burned with the result that this species combination is greatly altered in some places and various

[1] Nomenclature of woody species is that of Rehder (1940).

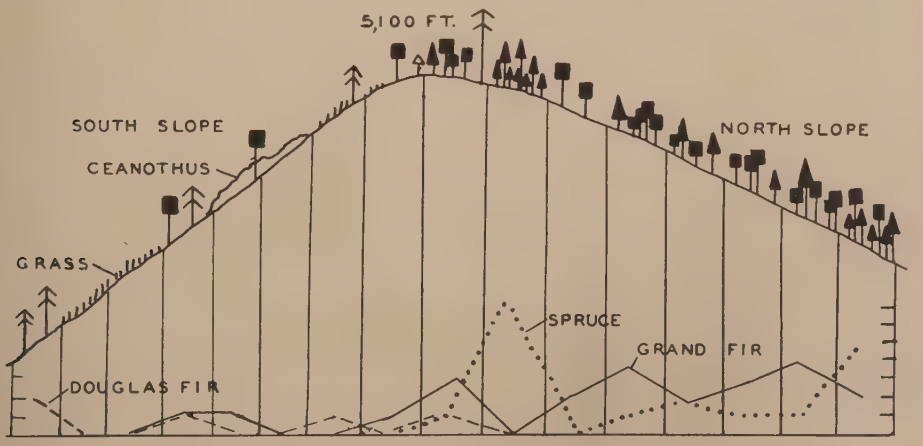

FIG. 6. Top of Moscow Mt. Same symbols as in Figure 3.

stages of succession are represented. In such areas, *Salix* spp., *Larix occidentalis*, and *Acer glabrum* var. *douglasii* are commonly found as dominants. On south slopes, *Pinus ponderosa* occurs in the drier sections and there is a trend to *Pseudotsuga taxifolia* and some *Larix* in the ravines. The presence of different successional stages again complicates the situation. Figure 3 shows that the pines are usually larger (and older) than the firs on the south slopes, a very common situation in certain parts of northern Idaho. Pine stumps five feet in diameter are found in the Gnat Creek area and yet the present forest is *Abies grandis* and *Thuja plicata*. Whether this trend is one caused by changing climate or by increased protection from fire is a matter of speculation.

Macro- and Microclimate

The climate of the Palouse Range is generally typical of the fringe of mountains which lie along the western edge of the Rocky Mountains in northern Idaho, at least as far north as the region of Lake Pend Oreille. The annual climate of the region exhibits two general seasons: the spring-summer season and the autumn-winter season. The first is characterized by a majority of clear warm days and cool clear nights. Since precipitation is low and evaporation and insolation high, drought may occur commonly during the late spring and especially in summer. Much of the moisture that is absorbed by plants is therefore derived from winter precipitation.

Most of the air associated with this kind of summer weather is of polar maritime origin but is more or less reduced in moisture by passing over the Cascades. If this air is relatively unstable, cumulus clouds may appear over the Palouse Range and develop into cumulo-nimbus clouds with rain and lightning. The tendency of such clouds to develop over the higher ridges reduces insolation and results in a slightly higher rainfall on these places.

TABLE II. *Moscow Mountain maximum and minimum temperatures at: (1) 2,770 ft. at Gnat Creek, (2) 4,100 ft. by the Potlach road; and (3) 4,450 ft. on the ridge, given in °F. Total snow depth in inches is given for each station at the end of the month indicated. Soil temperature is given in °F. for 4 in. depth under a canopy as measured once at the end of each month shown. Data of 1950–1951*

Elevation (feet)		2,770	4,100	4,450
Nov.	Min.	29	17	—
	Max.	49	46	
	Snow	0	0	0
	Soil temp.	46	46	45
Dec.	Min.	9	13	8
	Max.	53	46	41
	Snow	7	13	24
	Soil temp.	33	33	33
Jan.	Min.	−4	−11	−13
	Max.	47	34	33
	Snow	5	30	32
	Soil temp.	33	32	33
Feb.	Min.	−2	−4	−10
	Max.	46	41	38
	Snow	6	30	36
	Soil temp.	33	32	33
Mar.	Min.	13	11	8
	Max.	66	49	48
	Snow	0	18	30
	Soil temp.	46	32	32
Apr.	Min.	21	20	14
	Max.	73	58	58
	Snow	0	0–3	3–18
	Soil temp.	46	45	33–45
May	Min.	28	29	28
	Max.	83	73	73
	Snow	0	0	0
	Soil temp.	48	48	48

In the autumn, often in early October, low pressure areas of considerable intensity begin to form over the relatively warm ocean west of the Washington coast or seem to bud off from the more extensive Aleutian low. These lows progress eastward usually just north of the Canadian border, but the fronts which are associated with them extend southward into the region in question.

Warm fronts associated with these lows are often not especially noticeable in their effects, but the cold fronts following the warm sectors are often quite sharp and the subsequent polar maritime

air is cold and unstable. After the front passes, there may be a large amount of snow or rain. Scattered fog resembling fracto-nimbus clouds then appears on the mountain sides below the general level of the cloud cover which ordinarily stands at about 3,900 feet. As the clearer air moves in behind this air mass the cloud level rises over the mountain to about 4,500 or 6,000 feet before breaking up. Figure 1 shows the range just after the passage of such a front; a heavy layer of ice has been deposited from the cloud layer on the trees. There may also be more precipitation in the upper parts of the mountain than in the lower parts during such a storm. Ten inches of new powder snow was measured in one January storm at 2,770 feet and 13 inches at 4,450 feet on the ridge just below Moscow Mountain. Snow depths during the winter are given in Table II.

At certain times in the winter, there are minor or entire invasions of polar continental air from the east side of the Rockies into the Moscow region, invasions which are not always shown on weather charts. Although such invasions may bring temperatures of $-30°$ F., their effect on soil temperature is often entirely ineffectual because of the insulating layer of snow. Soil temperatures near the surface fall little or not at all below the freezing point if covered with snow (Table II). On the lower south slopes, however, the snow may melt off in late March or April and then the soil sometimes becomes frozen for a few inches in depth while the snow-covered north slopes remain unfrozen.

The frequently cloudy days of late autumn and winter result in little local heating effects on different slopes. However, there is often a cold air drainage down the mountain ravines during any of the months of the year and especially in the clear nights of autumn when outward radiation is quite marked. This air drain-

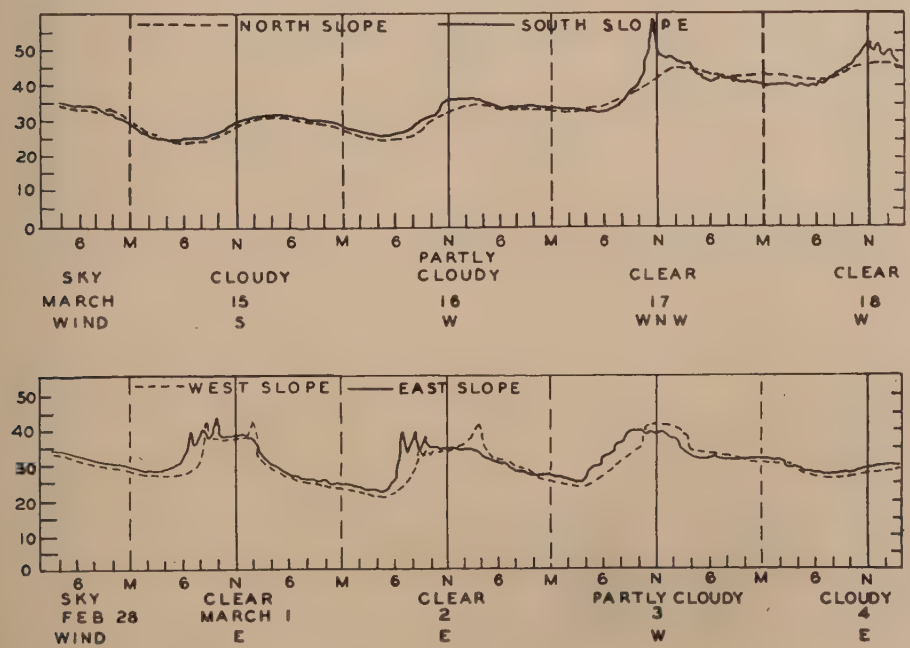

FIG. 7. Thermograph recordings (in °F.) on north and south slopes and east and west slopes of Gnat Hill during a period in the autumn-winter season.

age seldom exceeds one mile per hour in velocity and cannot be measured with standard type anemometers with any accuracy. How much this drainage affects the vegetation along ravines is hard to say since soil moisture effects are of great importance.

Air temperatures generally decrease with altitude, but exceptions to this sometimes occur (Table II). This may be caused by the air drainage effect. Air temperatures on north and south slopes are illustrated in Figures 7 and 8 for the two general types of weather and do not show as much temperature difference between slopes as one might expect. The thermometer elements were sheltered and were only 3 inches over the ground so that if differences between slopes occur it should show up best in the air near the ground (Geiger 1950: 181).

Soil temperatures sometimes show marked differences on north and south slopes at 3 to 6 inches depth and as much as 20 degrees difference is not uncommon on an open south slope and a forested north slope in spring. However, soil temperatures vary widely on a south slope between forest and open pasture land and the spring flower aspects can be seen to be retarded under the tree canopies.

High soil temperature has the effect of raising the vapor pressure difference between the soil and air and probably also favors higher transpiration by increasing water absorption by roots. Higher transpiration on south slopes is also favored by greater insolation and certain other factors including higher wind velocities. Weaver (1914) found that evaporation from atmometer bulbs was considerably higher on south slopes forested with *Pinus ponderosa* on the western end of the Palouse Range at the Viola Grade than on the north slopes in *Pseudotsuga* and *Larix*.

As a result of these effects, and also because the snow cover melts (and evaporates) on south slopes faster than on north in spring, soil moisture falls more rapidly

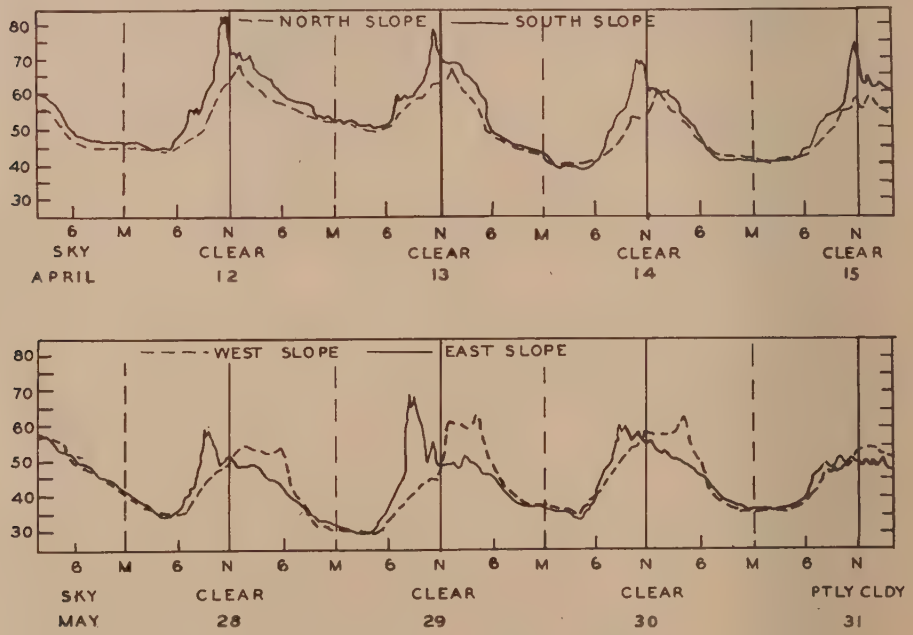

FIG. 8. Thermograph recordings in the same places as in Figure 7 but made during the spring-summer season.

TABLE III. *Percentage soil moisture on Moscow Mountain and adjacent hills with moisture equivalents and xylene equivalents*

	Topographic location	Horizon	East Twin (4,550)				Gnat Hill (3,870)				Moscow Mountain (5,100)			
			H_2O Apr. 21	H_2O May 25	M.E.	X.E.	H_2O Apr. 10	H_2O May 27	M.E.	X.E.	H_2O May 29	M.E.*	M.E.	X.E.
South slope	100 ft. down from top	A	32.8	26.4	35.4	16.9	23.2	27.3	28.0	11.5	14.2	15.5	25.4	10.0
		B	13.8	21.9	23.3	10.0	13.7	19.9	22.0	9.2	10.5	14.8	21.2	9.9
	50 ft. down from top	A	37.9	11.7	28.0	11.5	28.6	33.4	21.2	9.9	18.0	15.5	22.7	8.5
		B	21.7	14.8	**	**	18.7	21.8	15.4	5.4	12.3	12.4	18.1	8.5
North slope	50 ft. down from top	A	62.6	59.4	42.4	16.0	71.9	56.1	47.0	17.5	48.7	52.9	47.2	20.7
		B	38.3	19.1	28.8	14.6	28.3	38.4	25.1	10.6	37.4	34.3	35.6	17.1
	100 ft. down from top	A	62.8	61.3	44.4	18.1	60.8	51.0	40.2	19.0	68.6	50.9	48.4	19.6
		B	63.0	38.7	35.3	15.2	56.7	24.9	22.4	10.4	59.5	43.3	39.0	18.7

* Unsieved, all other X.E.s and M.E.s sieved.
** Rocky.

to the wilting point on south slopes than on north slopes. Since water-holding-capacity of south slope soils is lower than north slope soils this effect is accentuated (Table III).

Relative humidity is, as would be expected, higher on north slopes than south on sunny days of late spring, but this may be partly the result of a denser forest cover on north slopes. Relative humidity may vary as much as 25 percent on the two slopes, but the difference is ordinarily less.

Wind velocity measurements on Gnat Hill (Fig. 3), a foothill to West Twin, showed only half again as much wind on south as on north slopes in April and May. Average wind velocities during April were 0.31 m.p.h. on the south slope and 0.21 m.p.h. on the north.

It appears that it is only on the higher slopes that wind plays an important role in affecting vegetation and in such places soil erosion and steepness of slope are also important factors in accounting for the sparseness of forest trees.

Soils

The Palouse Range, including East Moscow Mt., Moscow Mt. itself (sometimes called Cedar Mt. elev. 5,100 ft.), East Twin, West Twin, and Paradise Point, is made up largely of a mass of light-colored granodiorite and related granitic rocks. The mass is sometimes referred to as the Thatuna Batholith to distinguish it from the more extensive Idaho Batholith to the eastward (Tullis 1944). This rock may be gneissic or porphyritic and is often intruded with quartz veins. The principal minerals of these rocks are quartz, feldspar, and biotite. One comparatively large quartz vein or veins is found along the ridge of Moscow Mt. and its low rate of weathering may account for this ridge standing higher than the adjacent hills.

The granitic rocks extend across the valley to the south almost as far as Tomer's Butte. To the north of the range, the valley is covered with Pliocene and Miocene lava flows overlain, sometimes rather thinly, with soil derived from this rock. In most cases, however, loess overlies the rocks, especially to the west of the range, and amounts to as much as 75 feet in depth in irregular hills. This loess also covers extensive areas near the base of the mountain where the underlying rock is granitic and is mixed with granitic-derived material at higher elevations.

Tullis (1944) dates the loess as Pleistocene but the dust drift seems to be occurring at the present time from semidesert regions in Washington as well as from the open-cultivated farm land nearby.

Thus, there are two general types of parent material, loess and weathered granitic rock. On the higher slopes of the Palouse Range, the soils are almost entirely derived from granitic material and are mostly gravelly loams. On these same slopes at similar elevations, however, there are patches of what appear to be loess, either almost pure or mixed with material derived from granitic rocks. It is possible that the wind removes the lighter soil material from the droughty south slopes, except in certain patches, thus leaving a more coarse gravelly soil over much of the area.

As far as we know, these soils are unnamed and unmapped except in the valleys where farm land seems to have warranted mapping. In addition to the gravelly loams found on many south slopes, silt loams occur commonly on north slopes. Another feature of many south slope soils is that they often contain an admixture of organic matter to a depth of about one foot, suggesting that in past centuries grass under pine or grass alone was the dominant vegetation. The north slope soils are usually finer in texture and hold more water (Table III), but the presence of mica distributed through the B horizon suggests that much of the parent material for this soil is granitic. There is evidently considerable loess mixed with it even at the highest elevations. Unlike those on the adjacent Tomer's Butte lying some 6 miles to the southward, the north slope soils do not usually have a very deep or at all pronounced organic layer in the surface horizon, probably because they have been in forest for past centuries and have become podzolic in character.

Depth of soil varies appreciably on any slope, the shallowest soils being found on the very steep south slopes such as near the top of West Twin or on Moscow Mountain. A survey of soil depth under about twenty 100–200 year old *Pinus ponderosa* trees showed that the depth varies considerably from tree to tree and is fairly well correlated with the site index as determined from tree age and height on charts worked out by Meyer (1934). In other words, the height of the trees for a given age corresponds to some extent to the depth of soil down to bed rock or to a closely-packed mottled soil.

Summary

In the Palouse Range of northern Idaho, the tree species show transitions from one habitat to another as one progresses along a compass line over varying topography. Considerable overlapping of one species into the region of another occurs, different species having different extents of distributional capability. *Abies grandis* and *Thuja plicata* are common on north slopes and ravines and *Pinus ponderosa* and *Pseudotsuga taxifolia* are common on south facing slopes. Altitudinal differences in vegetation are also evident on the Range with *Picea engelmanni* occurring in mixture with *Abies grandis* and sometimes with *Thuja plicata* and *Larix occidentalis* at the higher elevations.

The climate is characterized by dry, clear summers and moist, cool, but not usually cold winters, so that the vegetation must rely on winter precipitation for much of its moisture supply. The microclimate varies widely on different slopes and seems to account for much of the difference in distribution of forest trees. Wind velocity is usually higher on south than north slopes, but not so much as is commonly supposed. Moisture is lost more rapidly from south slopes in winter from the snow cover itself and from the soil and vegetation especially in spring and summer so that the soil reaches the wilting point more rapidly on south than on north slopes. As a result of these effects, the more xerophytic trees occur on the south slopes, the more mesophytic on north slopes or near streams.

The underlying rocks in the range are more or less similar in composition but

aeolian material is common in these soils and varies widely in occurrence. South slope soils are generally more coarse-textured and hold less available water whereas north slope soils are finer textured and hold more available water. Depth of soil was found to be related to the site index of individual *Pinus ponderosa* trees on south slopes.

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COMPARATIVE RATES OF DEHYDRATION AND HYDRATION IN SOME CALIFORNIA SALAMANDERS[1]

NATHAN W. COHEN[2]

Museum of Vertebrate Zoology, University of California, Berkeley

INTRODUCTION

Because of their abundance and differences in habits, salamanders in the San Francisco Bay region are well suited to an ecophysiological study. Their marked dependence upon physical factors, such as water, humidity, and temperature, further enhances their value for such investigations. The purpose of the present undertaking is to relate the nature of water regulation in the several forms studied to their behavior and occurrence.

The animals selected were two wholly terrestrial plethodontid salamanders, *Ensatina eschscholtzii xanthoptica* Stebbins, a ground dweller, and *Aneides lugubris lugubris* (Hallowell), of semi-arboreal habits, and a salamandrid, *Triturus torosus* (Rathke), a species that is aquatic during the breeding season.

The technique employed in the study was to measure rates of water loss and gain under controlled conditions of dehydration and hydration. The investigation was primarily concerned with conditions salamanders would most probably encounter in nature rather than the extremes of vital limits. Therefore the animals were not dehydrated to the extent of approaching the lethal limits.

This work was carried out under the guidance of Professor Robert C. Stebbins and was aided by advice and suggestions of Professors S. F. Cook and Oliver P. Pearson.

MATERIALS AND METHODS

The dehydration apparatus (Fig. 1) consisted of a cotton baffle - anhydrous calcium chloride air filter which removed moisture and cleaned the air. This unit was connected to an airflow meter by which a constant rate of air flow was maintained. The air passed from the flow meter into 15 feet of coiled copper tubing immersed in a constant temperature water bath. Submerged in this water bath was the dehydration chamber, which consisted of the lower half of a Scheibler desiccator (2″ depth, 4″ diameter, 630 cc. total volume of lower half) into which the dried and cleaned air was directed. The animals were confined within the flow of air by means of wire screening, which also prevented them from coming into contact with any glass surface except the bottom of the desiccator. Air and water temperature were checked by means of thermometers inserted into the water bath, air line, and desiccator. Dehydration was carried out at 20° C. ± 1°.

The hydration apparatus (Fig. 2) consisted of a circular glass vessel (2½″ depth, 8″ diameter) which was filled to a level of 1″ with clean quartz sand. The sand was covered with several layers of paper towels. Water entered and emptied out of the vessel ½″ below the surface of the sand. The rate of water flow into the hydration chamber was controlled by an adjustable clamp and was maintained at the minimum rate needed to maintain the desired level at ½″ below the surface. The level was checked against a mark at the ½″ level on the outside of the vessel, and a small screened area held the sand back on the inside to permit a clear view of the water. Capillarity of the sand continuously brought water to the surface, thus keeping the paper towels saturated.

According to Adolph (1943), frogs which are partly dehydrated will not recover water in air saturated with mois-

[1] A thesis submitted in partial fulfillment of the requirements for the degree Master of Arts, at the University of California.

[2] Presently of the Department of Biology, Fresno State College, Fresno, California.

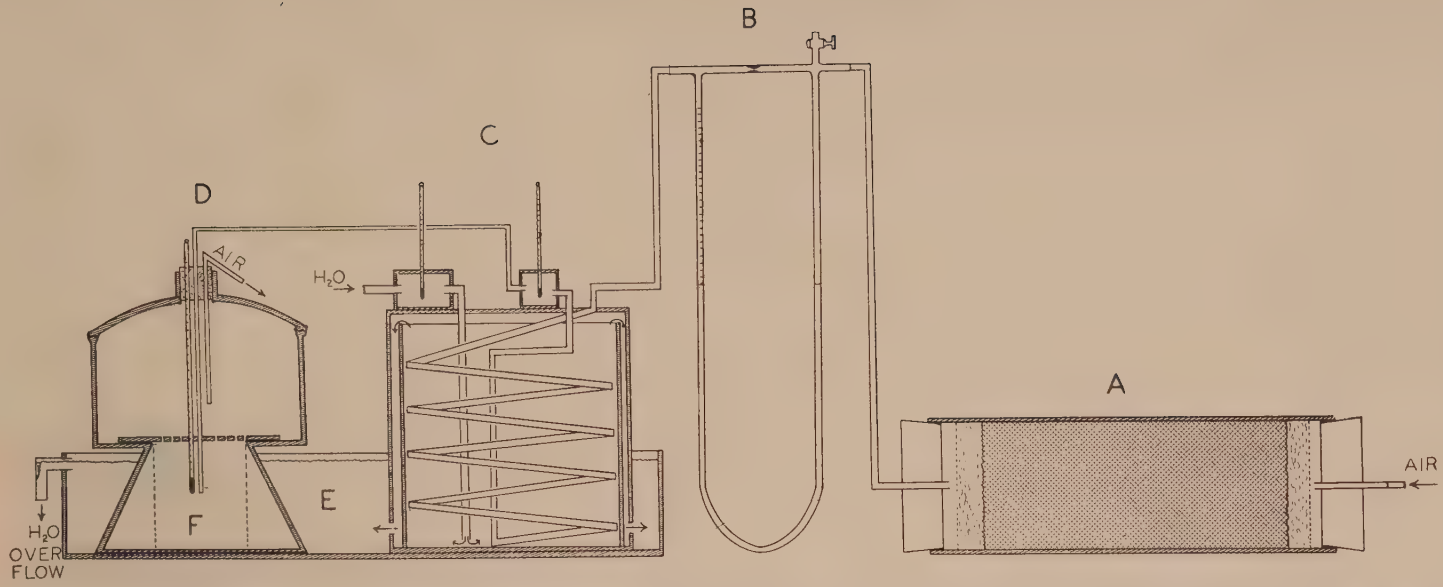

FIG. 1. Dehydration apparatus. A, calcium chloride tube; B, air-flow m eter; C, temperature regulator with thermometer indicators of temperature of air and water; D, Scheibler vessel with dehydration chamber (F); E, water bath for dehydration chamber.

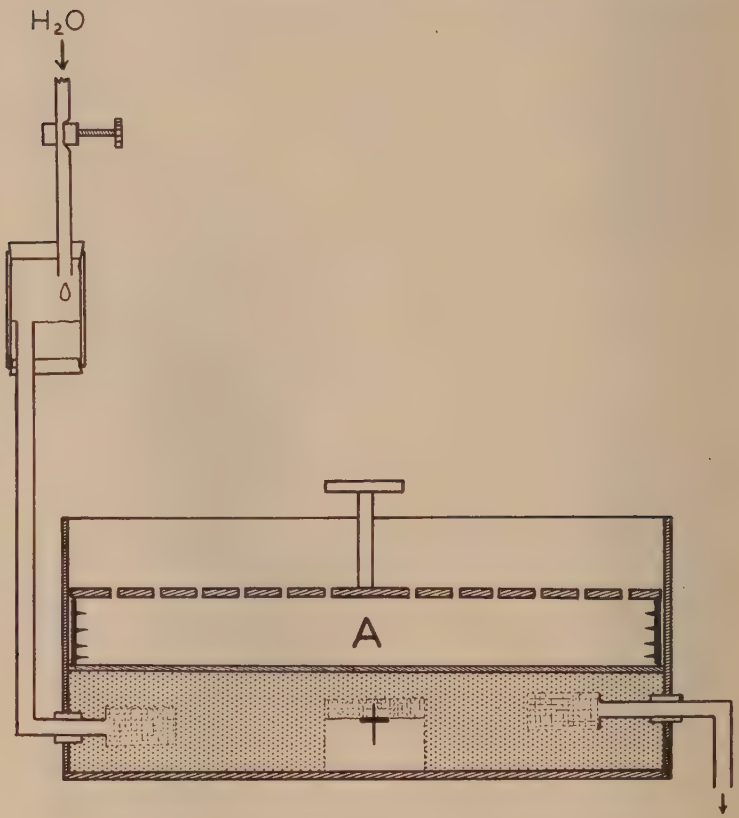

Fig. 2. Hydration apparatus. Animals were placed in area marked A. Sand is represented by stippling.

ture. Because of possible differences in water regulation between anurans and salamanders, however, the hydration chamber was equipped with a plastic lid in which there were a number of perforations to permit the escape of water vapor at a rate sufficient to prevent condensation of moisture within the vessel. Due to the evaporation through these perforations, no free water (*i.e.* pools) formed on the surface of the towels.

Because of the tendency of some of the salamanders to cling to the sides of the vessel and to avoid the moist surface of the towels, it was necessary to place on the inside wall of the vessel a plastic collar with copper-plated tacks protruding toward the interior of the vessel; the tacks effectively kept the animals on the moist surface of the chamber.

The hydration apparatus was kept in a room of 51 to 60 percent relative humidity and a constant temperature of 13° C.

Possible ecotypic physiological differences within a species were avoided by procuring all the individuals from the same general locality. *Ensatina* were obtained in a small canyon on the edge of a redwood (*Sequoia sempervirens*) stand, near Canyon, Contra Costa County. *Aneides* were taken from fissured rock walls at two localities less than ½ mile apart, at Berkeley, Alameda County, and *Triturus* in the aquatic stage were obtained from one area in Wildcat Creek, Contra Costa County. Only aquatic adult or nearly adult animals were used.

Only one or two animals were obtained at a time and were put into jars with a little of the substratum on which they were found or water in the case of *Triturus*. The animals were taken immediately to the laboratory and kept in the jars at a temperature of 13° C. until they were used for experimentation; ordinarily this interval did not exceed one day. Littleford, Keller, and Phillips (1947) demonstrated that salamanders could be kept in a moist container in a refrigerator (temperature not stated) for a 48-hour period without such storage producing any significant difference in the results of dehydration experiments.

Observations on the salamanders in their natural environment and in the laboratory suggested that their respective behavior patterns might play an important part in the experimental results. Field and laboratory behavior was therefore recorded and has been of aid in the interpretation of the experimental findings. This topic is discussed beyond under the "discussion."

Numbers of individuals used were as follows:

	Males	Females	Sex not determined	Total
Ensatina	3	7	1	11
Aneides	4	13	3	20
Triturus (aquatic)	8	1	2	11

Throughout the course of experiments, the animals were weighed in a thin, porous silk bag on a long-arm balance accurate to 1 milligram. Before the first weighing, adhering substratum was removed from the animals by gentle brushing, and the wet *Triturus* were momentarily wrapped in a soft, absorbent cloth. Thereafter, dehydrating individuals were not dried prior to weighing, and hydrating animals were merely put on a piece of filter paper for an instant in order to remove excess water before each weighing. The weight of the silk bag containing the animal was determined before each weighing.

Dehydration. In order to compare rates of water loss, it was necessary to consider the following physical factors: (1) air temperature, (2) rate of air flow, (3) humidity, (4) volume of the dehydration chamber, and (5) duration of dehydration. All these factors, plus those of pressure and illumination, affect the process of evaporation (Shelford 1913). Pressure was atmospheric and illumination was negligible since the dehydration chamber was covered and submerged in water.

The time required to reduce the weight of the animals by 20 percent was chosen to be the variable factor. Air temperature was kept at 20° C. ± 1.0°, rate of air flow was maintained at 1,700 cc. per minute. Experimentally, this rate was found to be considerably less than the maximum that any of the three species could safely endure for the period of dehydration. It is well known that fast rates of dehydration in amphibians produce deleterious effects, while slower rates result in a greater loss of body water before such harmful effects become manifest (Shelford 1913; Littleford *et al.* 1947; Thorson and Svihla 1943). Equally as important as the rate of air flow is the velocity of the air immediately around the animal. This factor depends principally upon the volume of the dehydration chamber and the placement of the animal within it. Humidity was not measured, but was maintained at a minimum by passing the air through calcium chloride. A test check was made, by using a phosphorus pentoxide trap, to determine the length of time the calcium chloride chamber was efficient in removing moisture from the air stream. Thereafter, the calcium chloride was replaced as often as this test indicated replacement was necessary. Size differences in the salamanders studied were considered insignificant compared to the total volume of the chamber. Preliminary investigation revealed that carbon dioxide eliminated through respiration had a negligible effect upon the results. Dehydrating animals were weighed at 1 to 2 hour intervals (for a total of 3

TABLE I. *Dehydration data*
Triturus torosus

Animal no. and sex	I Orig. body wt. (gm.)	II Time of 20% loss (mins.)	III gm. H_2O lost/hr.	IV gm. H_2O lost/hr./ gm. b. wt.	V Skin condition
1 ♂	10.20	218	.56	.05	S
2 ♂	11.03	240	.55	.05	R
3 ♂	11.57	220	.63	.05	S
4 ♂	12.76	238	.62	.05	S
5 ♂	13.24	240	.66	.05	R
6 ♀	14.59	242	.72	.05	R
7 —	14.77	228	.78	.05	R
8 ♂	15.49	368	.51	.03	S
9 —	15.80	252	.75	.05	S
10 ♂	15.94	299	.64	.04	R
11 ♂	17.52	280	.75	.04	S
Means	13.90	257	.65	.05	

S—predominantly smooth.
R—predominantly rough.

or 4 weighings) until they had given up at least 20 percent of their body weight.

After a salamander had been reduced 20 percent or more in weight, it was placed in a small covered petri dish and allowed to remain overnight at 13° C. This interval permitted any potential deleterious effects of dehydration to appear. If such effects were evident the following day, the animal was not used for hydration experiments; harmful effects were seldom noticed. It was noted, however, that a small, additional loss of weight took place by evaporation during this interval. This observation coincides with that of Adolph (1943) who found that in frogs with a water deficit, a very slow loss of water continues by evaporation even in air saturated with water vapor.

Hydration. Rate of hydration was determined by placing a salamander within the hydration chamber and weighing the animal at fairly regular intervals, the frequency of weighings depending upon the rate of hydration.

Hydration was usually terminated shortly after the animal regained its original weight, but some individuals were kept in the chamber longer so that any fluctuations in weight thereafter could be recorded.

TABLE II. *Dehydration data*
Aneides lugubris

Animal no. and sex	I Orig. body wt. (gm.)	II Time of 20% loss (mins.)	III gm. H_2O lost/hr.	IV gm. H_2O lost/hr./ gm. b. wt.
1 ♀	3.66	240	.18	.05
2 —	5.65	204	.33	.06
3 —	5.68	287E	.24	.04
4 —	5.82	231	.30	.05
5 ♀	5.93	211	.34	.06
6 ♀	6.34	178	.43	.07
7 ♀	7.45	208	.43	.06
8 ♂	8.04	180	.54	.08
9 ♀	8.88	250	.43	.05
10 ♀	8.93	267	.40	.04
11 ♀	8.99	331	.33	.04
12 ♂	9.04	278	.39	.04
13 ♀	9.26	256	.43	.05
14 ♀	9.64	319	.36	.04
15 ♂	9.70	262	.44	.04
16 ♀	10.07	289	.42	.04
17 ♀	10.07	272	.44	.04
18 ♀	10.47	292	.43	.04
19 ♂	10.53	260	.49	.05
20 ♀	15.21	408	.45	.03
Means	8.47	261	.39	.05

(E—curve extended by approximation.)

TABLE III. *Dehydration data*
Ensatina e. xanthoptica

Animal no. and sex	I Orig. body wt. (gm.)	II Time of 20% loss (mins.)	III gm. H_2O lost/hr.	IV gm. H_2O lost/hr./ gm. b. wt.
1 ♀	2.96	139	.25	.08
2 ♀	4.57	128	.43	.09
3 ♀	5.15	244	.25	.05
4 ♂	5.23	149	.42	.08
5 ♂	5.52	149	.44	.08
6 ♀	5.72	200	.34	.06
7 ♂	6.13	129	.57	.09
8 ♀	6.31	207	.36	.06
9 ♀	6.39	166	.46	.07
10 ♀	7.10	258	.33	.05
11 —	7.19	264	.33	.05
Means	5.66	185	.38	.07

EXPERIMENTAL DATA

The dehydration data appear in Tables I, II, and III. The calculations in Column II of each of these tables were derived from the graphs in Figure 3. The dehydration curves for all three species were essentially straight lines, except for minor

deviations due to experimental error. Thus, in each species, the rate of water loss during the reduction of the animal to 80 percent of its original weight appears to be constant, a finding which coincides with Hall's (1922) work on *Ambystoma punctatum* (L.) and with that of Littleford *et al.* (1947) on some plethodontid salamanders.

Dehydration results. The animals listed

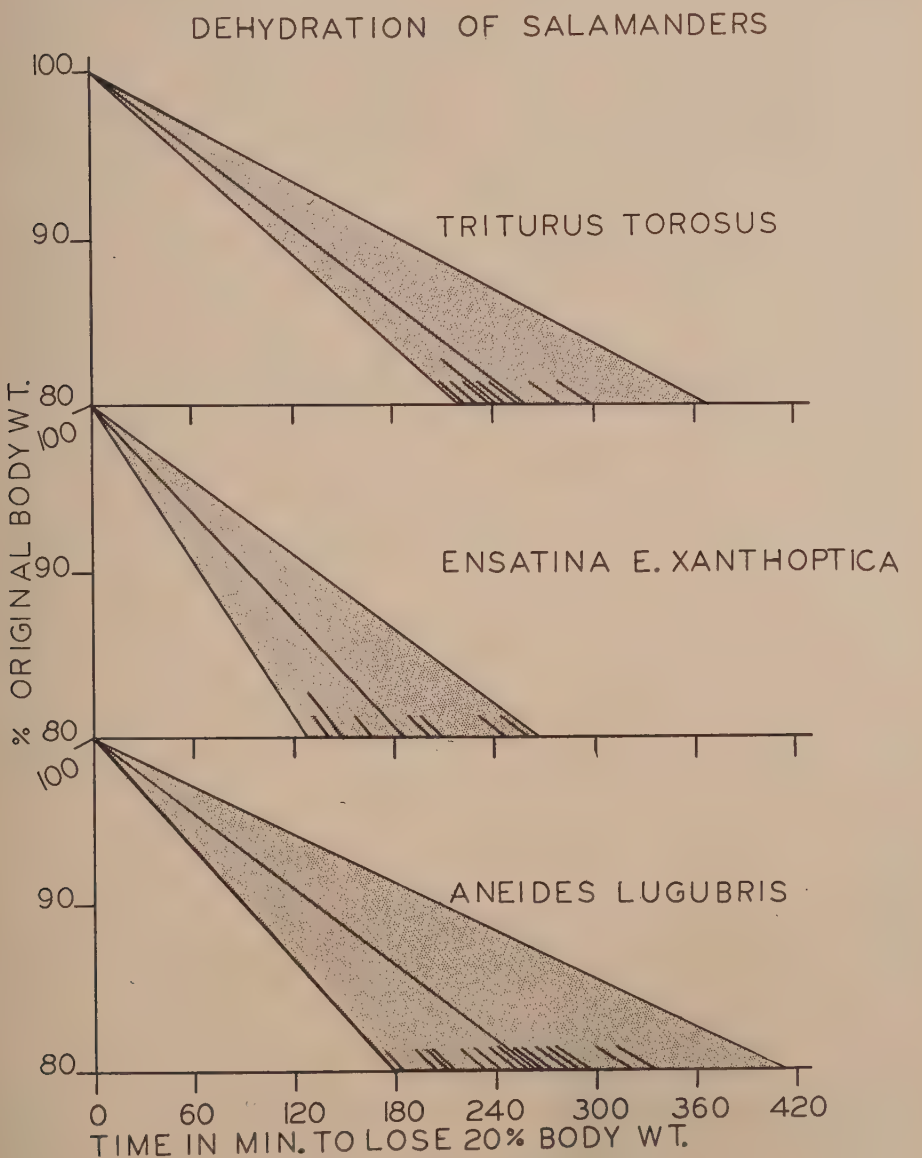

FIG. 3. Dehydration of salamanders. The lines extending from 100 to 80 percent represent the extremes and means in time to lose 20 percent body weight. Each short bar indicates an individual. Bars double in length represent two individuals.

in Tables I, II, and III are arranged in order of increasing weights, and the mean weights and range of variation appear in Table IV—A. Ranges and variations in dehydration results appear in Table IV—B, C, D. Male *Triturus,* late in the aquatic stage, showed variation in the condition of the skin, from predominantly smooth to predominantly rough, but no correlation was found between the rates of water loss and skin condition (Table I, Column V). Likewise, no significant correlation was found between the rates of water loss and body size. The mean time to lose 20 percent of the body weight was 4 hours and 17 minutes. In terms of grams of water lost per hour per gram of body weight the mean was .05 grams of water (Fig. 4).

Dehydration results in *Aneides* were similar to those obtained for *Triturus.* In *Aneides* no positive relationship appears between body weight and time to lose 20 percent of the body weight (mean time was 4 hours and 21 minutes), nor between original weight and grams of water lost per hour per gram body weight (mean was .05 grams of water, Fig. 4).

Ensatina shows the same lack of correlation both between body weight versus time to lose 20 percent (mean time was 3 hours and 5 minutes) and between original body weight and grams of water lost per hour per gram of body weight (mean was .07 grams of water, (Fig. 4).

Within any one of the three species, then, very little, if any, correlation between body size and rate of water loss could be demonstrated. These results agree with those of Littleford *et al.* (1947) who found in a series of plethodontids essentially the same lack of correlation between body weight and rate of water lost.

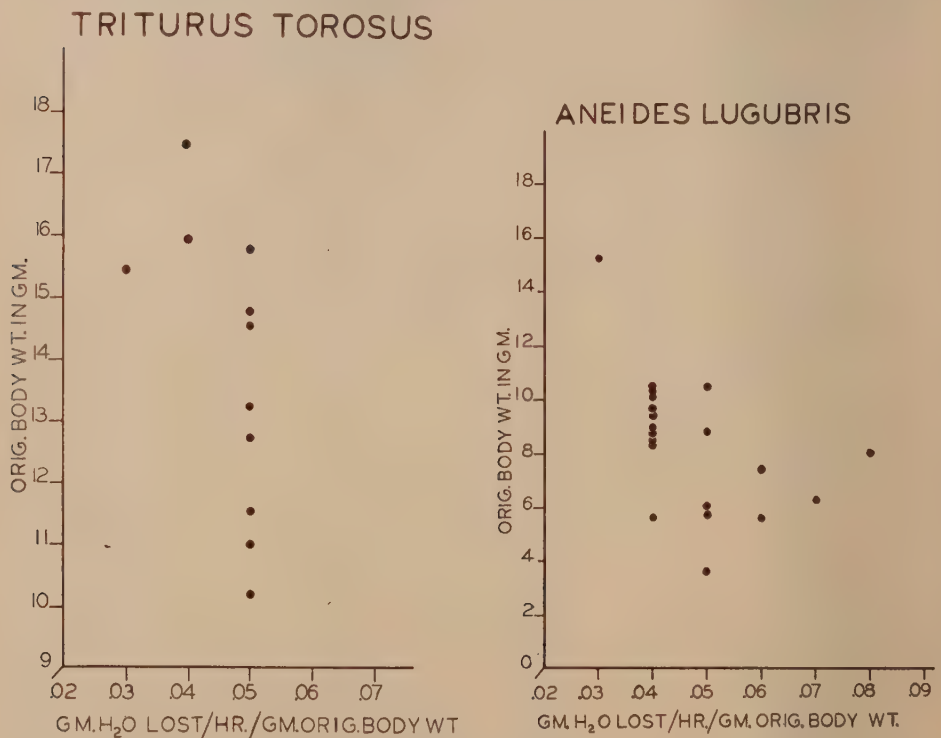

FIG. 4. Scatter diagrams indicating degree of correlation between body weight and rate of water loss.

Comparisons among the three species, rather than between individuals of one species, however, do show some interesting differences in rates of water loss. In regard to differences among species one might expect, on the basis of size alone, a larger species to take a longer time than a smaller one to lose the same percentage of body weight through evaporation of water from the surface of the skin because of the surface-mass relationship. Although *Triturus* is considerably larger than *Aneides,* the latter required a slightly longer time to lose 20 percent body weight. Between the two plethodontids, however, a relationship between body size and rate of water loss appears to be borne out. The data show that the *Aneides* are about 30 percent greater in mean weight than the *Ensatina* and that *Aneides* requires approximately 30 percent longer, on the average, to lose the same percentage of water. It is doubtful, however, that this is a correlation related solely to size differences between the two species. Even though the mean difference in body weight

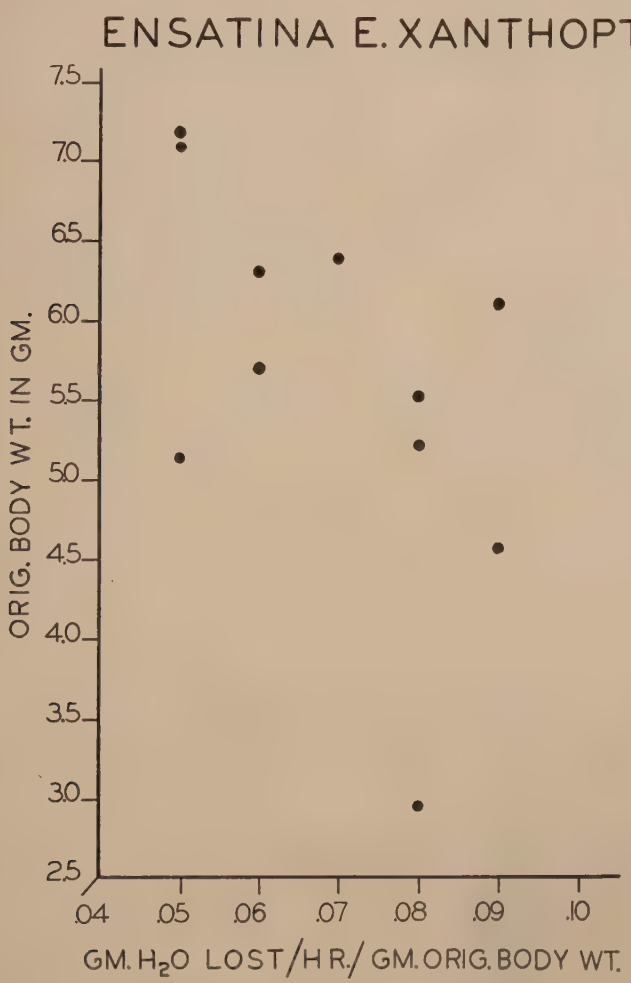

Fig. 4.—*Continued.*

TABLE IV. *Summary of dehydration data*

A

Original body weights (grams)

	Mean	Max.	Min.	Range
Triturus	13.90	17.52	10.20	7.32
Aneides	8.47	15.21	3.66	11.55
Ensatina	5.66	7.19	2.96	4.23

B

Time of 20% body wt. loss (minutes)

	Mean	Max.	Min.	Range
Triturus	257	368	218	150
Aneides	261	408	178	230
Ensatina	185	264	128	136

C

Grams of water lost per hour

	Mean	Max.	Min.	Range
Triturus	.65	.78	.51	.27
Aneides	.39	.54	.18	.36
Ensatina	.38	.57	.25	.32

D

Grams of water lost per hour per gram of body weight

	Mean	Max.	Min.	Range	S.D.	S.E.
Triturus	.05	.05	.03	.02	.0024	.00073
Aneides	.05	.08	.03	.05	.0123	.0028
Ensatina	.07	.09	.05	.04	.0158	.0048

E

Difference between means of grams of water lost per hour per gram of body weight (critical ratios or "*t*" values)

Ensatine-Aneides	3.68
Aneides-Triturus	0.00
Ensatina-Triturus	7.04

between *Triturus* and *Aneides* is almost two times greater than the mean difference in body weight between *Aneides* and *Ensatina,* the former pair show no difference in rates of water loss in grams per hour per gram of body weight, while the latter pair show a significant difference. The critical ratio of the means or "*t*" value

$$\left(t = \frac{x_1 - x_2}{\sqrt{SE_1^2 + SE_2^2}}\right)$$

of dehydration in terms of water lost per hour per gram of body weight (Table IV—D) appears in Table IV—E.

Hydration results. The hydration data were treated essentially in the same manner as the dehydration results. The same individuals were used in dehydration and hydration. Hydration data appear in Tables V, VI, and VII. The figures in Column II of each of these tables were obtained from a graph upon which the

TABLE V. *Hydration data*
Triturus torosus

Animal no. and sex	I Orig. body wt. (gm.)	II Time of 10% gain (mins.)	III gm. H_2O gained/ hr.	IV gm. H_2O gained/ hr./gm. b. wt.	V Skin cond.
1 ♂	10.20	1210	.050	.010	S
3 ♂	11.57	2760	.025	.004	S
4 ♂	12.76	800	.090	.014	S
5 ♂	13.24	574	.140	.021	R
6 ♀	14.59	2026E	.045	.006	R
8 ♂	15.49	1105	.085	.011	S
9 —	15.80	1505	.065	.008	S
10 ♂	15.94	1060	.090	.011	R
11 ♂	17.52	1745	.060	.007	S
Means	14.12	1421	.070	.005	

E—curve extended by approximation.
S—predominantly smooth.
R—predominantly rough.

TABLE VI. *Hydration data*
Aneides lugubris

Animal no. and sex	I Orig. body wt. (gm.)	II Time of 20% gain (mins.)	III gm. H_2O gained/hr.	IV gm. H_2O gained/hr./ gm. b. wt.
1 ♀	3.66	566	.08	.02
6 ♀	6.34	143E	.53	.08
7 ♀	7.45	265	.34	.04
8 ♂	8.04	1077E	.09	.01
9 ♀	8.88	207	.52	.06
10 ♀	8.93	279	.38	.04
11 ♀	8.99	324	.33	.04
12 ♂	9.04	585	.19	.02
13 ♀	9.26	380	.29	.03
14 ♀	9.64	600	.19	.02
15 ♂	9.70	287	.40	.04
16 ♀	10.07	186	.65	.06
17 ♀	10.07	371	.32	.03
18 ♀	10.47	765E	.16	.02
19 ♂	10.53	1185E	.11	.01
20 ♀	15.21	935E	.20	.01
Means	9.14	510	.30	.04

(E—curve extended by approximation.)

percent of original body weight gained by each salamander was plotted against time in minutes. Ranges and variations of hydration results are summarized in Table VIII. The most striking feature of the study on *Triturus* was that only 3 of a total of 9 individuals regained their original weight. The other 6 animals eventually reached an equilibrium in weight or began to lose weight between 90 and 100 percent original weight. Results for *Triturus,* therefore, were computed on the basis of the gain from 80 to 90 percent original weight, thus including only that part of the curve in which steady gain in weight was evident for all individuals (Fig. 6). The scatter diagram for *Triturus* (Fig. 5) indicates the lack of correlation between rate of water gain and size of animal. The mean grams of water gained per hour per gram of body weight was 0.005.

The curves representing the rates of hydration for the plethodontids were computed on the basis of the gain between 80 and 100 percent original weight (Fig. 6). In *Aneides* and *Ensatina* the lack of correlation between rate of gain and body size is indicated in Figure 5. The mean rate of water absorption in grams per hour per gram body weight was 0.04 in *Aneides* and 0.015 in *Ensatina.*

Thus far it appears that there is, among individuals of any one of the three species, no relationship between body size and

TABLE VII. *Hydration data*
Ensatina e. xanthoptica

Animal no. and sex	I Orig. body wt. (gm.)	II Time of 20% gain (mins.)	III gm. H_2O gained/hr.	IV gm. H_2O gained/hr./ gm. b. wt.
1 ♀	2.96	364	.10	.034
2 ♀	4.57	1935	.03	.006
3 ♀	5.15	978	.06	.012
4 ♂	5.23	1282	.05	.010
6 ♀	5.72	886	.08	.014
7 ♂	6.13	1270	.06	.010
8 ♀	6.31	604	.12	.019
9 ♀	6.39	838	.09	.014
10 ♀	7.10	967	.09	.013
11 —	7.19	625	.14	.019
Means	5.80	975	.08	.015

TABLE VIII. *Summary of hydration data*

A

Original body weights (grams)

	Mean	Max.	Min.	Range
Triturus	14.12	17.52	10.20	7.32
Aneides	9.14	15.21	3.66	11.55
Ensatina	5.80	7.19	2.96	4.23

B

Time of gain of body wt. (mins.)

	Amount of gain	Mean	Max.	Min.	Range
Triturus	(10%)	1421	2760	574	2186
Aneides	(20%)	510	1185	143	1042
Ensatina	(20%)	975	1935	364	1571

C

Grams of water gained per hour

	Mean	Max.	Min.	Range
Triturus	.07	.14	.025	.115
Aneides	.30	.65	.08	.57
Ensatina	.08	.14	.03	.11

D

Grams of water gained per hour per gram of body weight

	Mean	Max.	Min.	Range	S.D.	S.E.
Triturus	.005	.021	.004	.017	.00224	.00074
Aneides	.040	.080	.010	.070	.02145	.00536
Ensatina	.015	.034	.006	.028	.00775	.00245

E

Difference between means of grams of water gained per hour per gram of body weight (critical ratios or "*t*" values)

Ensatina-Aneides	4.24
Aneides-Triturus	6.55
Ensatina-Triturus	3.90

rates of absorption of water. The relationships between body size and rate of water gain that may exist *among* the species are of interest. *Triturus,* the largest of the three species, requires the longest time to regain its weight. However, it is clear that factors other than body size are involved since *Triturus* is only one-third greater in mean body weight than *Aneides,* but the latter absorbed, per hour per gram of body weight, eight times the amount of water absorbed by the newt. A comparison between individual *Aneides*

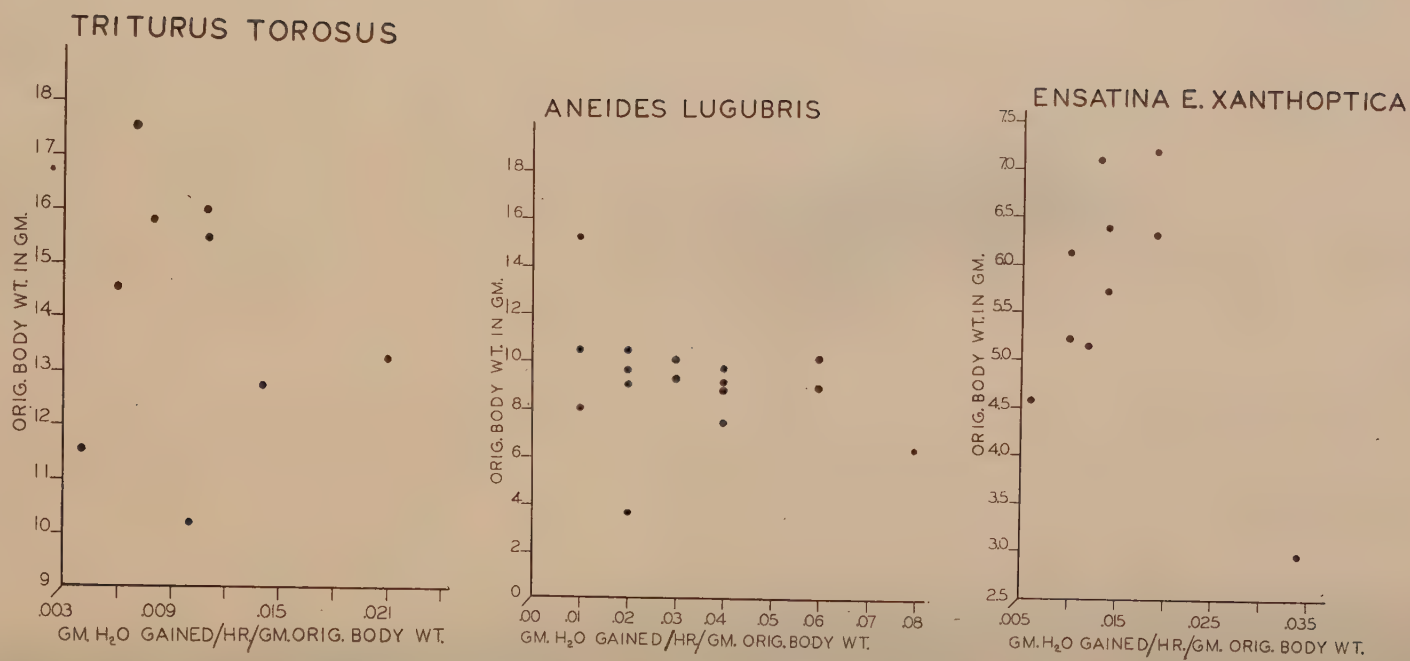

FIG. 5. Scatter diagrams indicating degree of correlation between body weight and rate of water uptake.

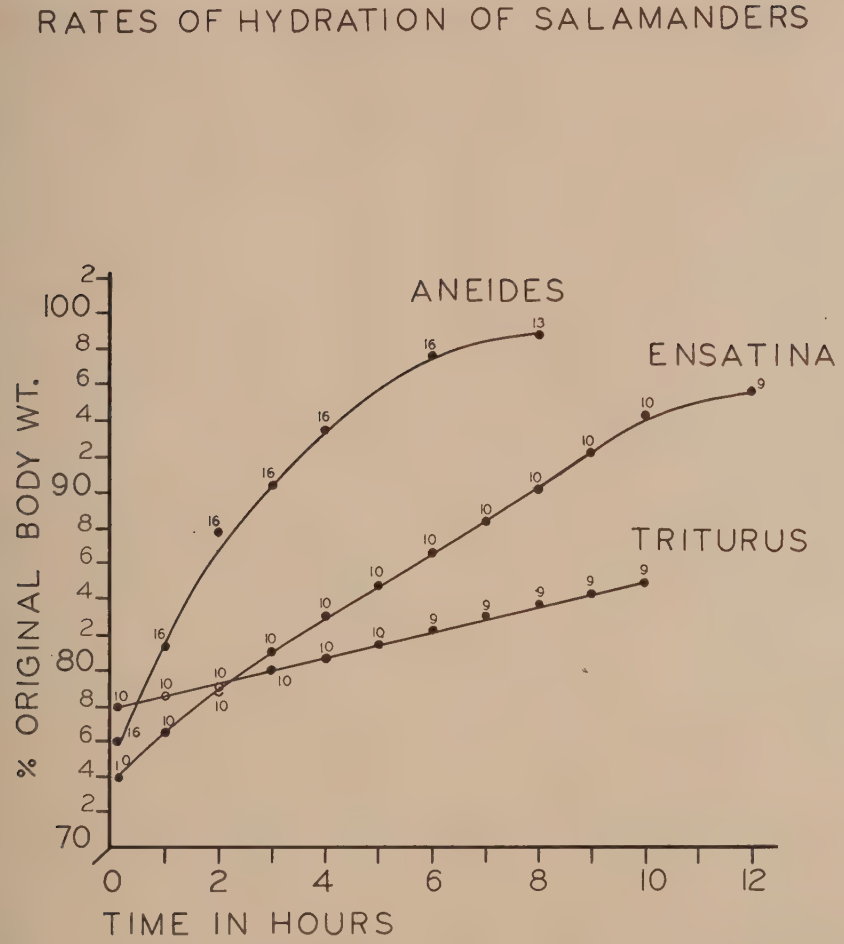

FIG. 6. Rates of hydration of salamanders. Curves represent the mean rate of water uptake in salamanders. Numbers above each point in the curves indicate the number of individuals used to derive the mean weight at that point.

and *Triturus* of nearly equal weights (Tables V and VI) further substantiates the conclusion that size is not the sole factor involved in this difference. In water gain per unit body weight in the plethodontids, *Aneides,* about 33 percent greater in body weight than *Ensatina,* absorbed water about 2.5 times faster than the latter (Table VIII—D).

Figure 6 presents the mean curve for hydration for each of the three species (gain within 80 to 100 percent body weight). The mean percentage of weight gained was calculated from the hydration curves of all the experimental animals of each species, and was plotted against time. Frequently the hydration experiment was terminated when an individual had regained its original weight; therefore the number of individuals (numerals above each point plotted on Fig. 6) involved in the mean values varied as original weight was approached.

Some individuals of each species, as noted earlier, were kept in the hydration chamber after having attained their re-

spective original weights in order to record the effect of extended exposure to moisture. In many instances, with the exception of *Triturus,* the amount of water absorbed exceeded the amount originally lost. In both *Aneides* and *Ensatina* as much as 10 percent above original weight was gained. Following the attainment of the original weight, elimination and absorption of water ordinarily resulted in an oscillation of body weight between 95 and 105 percent of the original weight.

A comparison of the critical ratios of mean rates of water loss (Table IV—E) and gain (Table VIII—E) shows the following: between *Ensatina* and *Aneides* there is a greater difference in rates of absorption than in rates of dehydration, as there is also in *Aneides* and *Triturus;* between *Ensatina* and *Triturus,* however, the difference is greater between the rates of water loss than in the rates of water gain.

By plotting the mean curves of hydration logarithmically, *i.e.,* log percentage of original weight versus log time

$$\left(\frac{\log W_{2-1}}{\log T_{2-1}} = k\right),$$

the following constants were obtained: (for the first 6 hours of hydration) *Triturus,* 0.0031; *Aneides,* 0.098; and *Ensatina,* 0.086.

In comparing the rates of dehydration and hydration in each species, the experimental difference in temperature in which the two phases of the study were conducted must be considered. Also the mean original weight for each species was slightly smaller in the dehydration experiments because of the elimination of some small animals in each group for the hydration experiments. However, by dividing the mean rate of water lost by the mean rate of water gained (Table IV—D and VIII—D), it is seen that aquatic stage *Triturus* loses water 10 times faster than it gains water, that *Aneides* loses only 1.25 times faster than it gains, and that *Ensatina* loses 4.66 times faster than it gains. These data suggest that rates of water loss and water gain in salamanders are different. Furthermore, *within* a species, as indicated in the following two examples, an individual salamander does not necessarily gain water at the same relative rate that it loses water. In *Aneides,* both individuals representing the extremes in water lost per hour per gram of body weight (.08 and .03 grams, respectively) absorbed water at the slowest rate (.01). (See Tables II and VI, individuals 8 and 20.) In *Ensatina,* the same animal which lost the greatest amount of water per hour per gram of body weight (.09) showed the smallest gain (.006) of water (Tables II and VII, individual 2).

Morphological Studies

The skin of frogs has been used in many physiological studies of osmosis and permeability; and among salamanders, especially in the eastern American species of *Triturus,* the skin has been studied principally in regard to the morphological changes brought about by the endocrine changes of these animals as they relate to the terrestrial-aquatic stages. Among the plethodontids little has been done in determining the relationship of microscopic structure of the skin to water regulation.

With this in view, a histological study was made of the skin of each of the three species of salamanders. Several individuals of both sexes of each species were used, and terrestrial as well as aquatic individuals of *Triturus* were compared.

The animals were freshly killed and the whole skin was cut and gently peeled back from the axillary region to the hind limbs. The body was then severed at the hind limbs, leaving only the posterior portion of the body and the inverted skin of the trunk. The skin was next turned back and the anterior opening was plugged with a small cork after the cavity had been filled with fixative. The skin was then immersed in fixative. Ten-micron sections were cut across the longitudinal axis so that all areas of the skin in the trunk region were represented. Hansen's Trichrome stain (Pantin 1936) was used.

In aquatic male *Triturus* it was observed that the skin is relatively unvascularized and lacking in the profusion of poison and mucous glands observed in the plethodontids. The epidermal layer is thickened, and the change that takes place when this species enters the water appears to be principally a modification of surface texture; the skin becomes practically devoid of tubercles and soft and leathery to the touch.

The skin of the two plethodontids is very similar morphologically. In both, the skin is not thickened and the dermal capillaries are most often covered by a very thin epidermal layer. The highly vascularized skin contains many mucous and poison glands interspersed among the capillaries. In *Ensatina e. xanthoptica,* the dermal capillaries are surrounded by lipophores which may retard the intake of water (Stebbins 1949). These fatty pigment cells may be present in the tail of *Aneides,* but seem not to be present, or are scarce, around the dermal capillaries of the venter of this animal.

Discussion

A study has been made of the rates of water loss and gain in *Triturus torosus, Aneides lugubris,* and *Ensatina eschscholtzii xanthoptica* in an effort to relate water regulation in the three species to their habits.

One of the results of the study has been the finding that within each species no correlation exists between body size and the rate of water loss or gain. Nor does there appear to be any direct relationship in individuals of a species between the rate of water loss and that of water gain. Since the surface-mass relationship does not appear as a significant factor in water regulation in these three species, an explanation of the experimental results must be sought elsewhere. Important factors to consider in water regulation are the habitat of the animals, their seasonal activity, their field and laboratory behavior, and their skin morphology. Metabolic rate, neural, endocrine, and other factors are no doubt involved in water regulation but they have not been investigated in regard to this phase in the life history of these salamanders.

Habitat and activity. Differences exist in the microenvironments inhabited by the three species, but the major habitat features are similar. Occasionally, the three forms are found together under apparently identical conditions of moisture and terrain.

Adult *Triturus torosus* spend part of each year, during the breeding season, in the water, and the remainder of the time on land, usually in moist surroundings in the vicinity of ponds, streams, and reservoirs, although they have been seen considerable distances from water or damp surroundings when in the terrestrial stage.

Aneides and *Ensatina* never enter the water as does *Triturus.* They are entirely terrestrial. *Aneides,* at times, is arboreal and is found mostly in coast live-oak trees (*Quercus agrifolia*). Its efficiency as a climber is indicated by its occurrence in the nest of a red tree mouse (*Phenacomys longicaudus*) at a height of nearly 60 feet (Benson and Borell 1931). During the late spring and early summer, it retreats underground, into hollows in logs, and into tree cavities. On the other hand, *Ensatina* is almost wholly a ground dweller and seems to avoid steep slopes.

Although the first heavy rains following the summer dry period bring all three species from their underground retreats, the animals differ in the span of their seasonal activity. In the areas studied, *Ensatina* becomes scarce shortly after the heavy rains of spring have ceased, whereas *Aneides* seems to have a somewhat longer period of activity. *Triturus* can be found still later in the season, sometimes extending its aquatic activities through July.

Between *Ensatina* and *Aneides* there is considerable similarity in seasonal activity; however, the microenvironment of the two species appears to differ in range of moisture content. I have always found

Ensatina in the East Bay area in moist situations and have seldom seen them in dry periods between rains. On the few occasions when *Ensatina* were so discovered, they were found in moist retreats. Bishop (1943) states, however, that *Ensatina* is found occasionally in fairly dry situations. *Aneides,* on the other hand, is frequently found upon surprisingly dry surfaces, sometimes at long distances (100 yards or more) from trees or leafy debris. During long periods of dry weather, between rains in winter and early summer, *Aneides* has often been encountered at night wandering on dry soil which would crumble in the hand. These encounters, however, generally occurred in the vicinity of established retreats, such as the crevasses of rock walls bordering irrigated gardens and lawns. On the basis of preliminary experiments with salamanders on a soil-moisture gradient (C. H. Lowe, Jr. MS), it appears that *Aneides lugubris,* on the average, selects slightly drier soil than *Ensatina e. xanthoptica.*

Observations on field and laboratory behavior. During the early phases of field and laboratory work, it appeared that the behavioral responses of the three species to environmental and laboratory conditions were generally species-specific. With the view that the distinctive reactions of these salamanders might have important bearing on water regulation, field and laboratory observations on behavior were recorded.

Aquatic *Triturus* are active, both day and night. Terrestrial individuals are occasionally active during the daytime, but commonly wander at night and seek shelter during the day under rotten logs, boards, rocks and in rodent burrows. During the daytime, the terrestrial newt is ordinarily found in a quiescent state under cover with its body resting on the ground. When so exposed it usually hesitates a moment, then lunges forward in an attempt to escape. Rarely is it found in a standing position while under cover.

Although the two plethodontids may be crepuscular to some extent, they have, unlike *Triturus,* seldom been seen abroad during the daytime, and are essentially nocturnal. Nocturnality provides the two plethodontids with at least two favorable conditions for lessening water loss through dermal evaporation: namely, the usually lower temperatures and the higher humidities occurring at night. The observation that *Aneides* seldom stands stiffly with its body off the ground, though it may occasionally do so when irritated, may be related to its arboreal and climbing habits. The arboreal habits of this salamander often place it in a more exposed position with respect to climatic factors than the strictly ground-dwelling species. The tendency, however, for *Aneides* to "hug" surfaces, thereby keeping its belly in close contact with the substratum, and to coil its tail when it is quiet, not only aids in lessening the amount of its body exposed to the air, but also facilitates dermal absorption of available moisture from the ground surface. The latter naturally applies equally to the other two salamanders.

When *Ensatina* is first exposed it may remain quiet for a few moments, then lunge forward to escape, or on exposure may assume a defensive posture. This posture, also assumed when the animal is irritated, is a stiff-legged stance with back arched downward and tail elevated.

Such variations in behavior patterns, as noted above among the three species, were also noted during the experiments, and are believed to have had some influence upon the experimental results. That is, during dehydration neither *Triturus* nor *Ensatina* was seen materially to reduce its respective body surface by coiling as did *Aneides,* although all three species kept their bellies in contact with the glass bottom of the experimental chamber. During hydration *Ensatina* was observed commonly in a standing position, whereas *Triturus* and *Aneides* seldom, if ever, assumed this stance.

In applying the above observations toward an explanation of the experimental results, the slow rate of water loss in *Aneides* may be explained, in part at least, by this animal's tendency to assume a tightly coiled position when exposed to drying conditions. Although the surface-mass relationship appears attractive as an explanation of the faster rates of water loss in *Ensatina,* it does not appear to be valid since no surface-mass correlation has been found within any of the species. The faster rates of loss in *Ensatina* may in part be due to less effective coiling when this species is exposed to dry air. Unlike *Aneides, Ensatina* seldom ventures into unfavorably dry climatic conditions. *Aneides,* however, is often exposed to drying air and reacts in a manner that tends to conserve water. As Storer (1925) states, "it has gone about as far as a non-aquatic salamander can go in the direction of terrestrial existence short of development of a dermal armor to check loss of moisture."

Again using behavior patterns as an explanation for rate differences, let us once more compare Aneides and Ensatina, this time considering the hydration data. The difference in rates of absorption between *Aneides* and *Ensatina* appears incongruous, because of (1) difference in body size, (2) similarity in skin structure, and (3) relative rates of water loss in dehydration. Although the ventral lipophores in *Ensatina* may interfere with water absorption, the main cause for the slower absorption in the smaller species is thought to be related to the defensive (or standing) position that *Ensatina* often assumed and maintained for long periods while within the hydration chamber. This position, described earlier, resulted in only the feet being in continuous contact with the wet towels. It is likely that this behavior may serve as a water regulatory mechanism in nature. Since *Ensatina e. xanthoptica* is most frequently found in moist situations, the simple expedient of raising or lowering the body would facilitate maintenance of body water equilibrium. It was often observed that even partly dehydrated *Ensatina* avoided the wet surface of the hydration chamber. The only reasons I can advance for this behavior are that the standing position is a genetically fixed response to excess moisture in the immediate surroundings of the animals or that the unnatural environment evoked the defensive posture. The fact that *Aneides* not only loses water at a slower rate than *Ensatina,* but also absorbs water at a faster rate, does not necessarily show that *Aneides,* in all respects, can maintain its body water at optimum better than *Ensatina.* It more clearly indicates that each species has developed behavioral and morphological adjustments to its respective type of environment.

Morphology. A dehydrating newt does not exhibit any specialized behavior pattern related to water conservation, and the relatively slow rate of water loss in *Triturus* is believed due to its thickened and relatively unvascularized skin. In the aquatic form there would seem to be no gain to the animal in having the ventral surface of the body specialized for water intake. Moreover, the histological change in the skin that occurs when *Triturus* enters the water is more likely to be a modification for further retarding water intake, a condition which would lessen the work of the excretory system in eliminating the excess.

An example of a difference in rates of hydration of two of the species of animals that may be attributed to morphology can be demonstrated by a comparison between *Triturus* and *Aneides.* These two animals behaved essentially alike in the hydration chamber, characteristically resting the entire ventral surface on the wet towels. *Aneides,* although one-third lighter in weight than *Triturus,* gained water eight times faster per gram of body weight than did the newt. The thin, vascularized skin of *Aneides* apparently offered comparatively little resistance to water absorption.

Although factors such as individual behavior patterns and skin morphology appear to exert a major influence upon the rates of water passage, an examination of the data does suggest that a correlation may be present between body size and rate of water absorption and loss. A surface-mass relationship probably does exist to some degree in all three species but is obscured by the above-mentioned factors. Factors, other than these, also may be involved in water regulation.

It is noteworthy that within the experimental range of loss and gain, rates of dehydration are constant (Fig. 3), whereas rates of hydration tend to decrease as original weight is approached (Fig. 6).

Summary

Salamanders of three species, *Ensatina eschscholtzii, Aneides lugubris,* and *Triturus torosus,* from the vicinity of Berkeley, California, were experimentally dehydrated and hydrated. The experimental results were expressed in grams of water lost (or gained) per hour per gram of body weight. The mean losses of water for each of the three species, expressed in the above terms, were the following: *Triturus,* .05; *Aneides,* .05; and *Ensatina,* .07. The mean gains in water were: *Triturus,* .005; *Aneides,* .040; and *Ensatina,* .015. It was demonstrated that within any one species there was no significant relationship between body size and rate of water loss or gain. No experimental relationship was found to exist between the rate of water loss and that of water gain, either among the species as a whole or within individuals.

The rates of water passage through the skin are regarded as being related primarily to the environmental conditions met by each species, structure of their body covering, and their behavior.

Gross habitat features are similar for all three species, but the microenvironment of each species may differ principally in respect to moisture content. Terrestrial *Triturus* have been found more often than the two plethodontids in dry situations, and appear to be more resistant to drying conditions than the latter. Of the plethodontids, *Aneides* seems to be less dependent upon moisture than is *Ensatina.*

A histological examination of the skin of the three salamanders revealed that in *Triturus* the difference between the skin of the terrestrial and aquatic forms is basically a modification of texture. In the terrestrial newt the skin has many minute tubercles giving it a rough texture, whereas the skin of the aquatic newt is practically devoid of tubercles and is soft and smooth to the touch. The epidermal layer is thickened, relatively unvascularized and has fewer mucous and poison glands than that of the plethodontids. The skins of *Aneides* and *Ensatina* are essentially alike morphologically, both being thin, highly vascularized, and profusely supplied with mucous and poison glands. Lipophores surrounding the ventral dermal capillaries in *Ensatina* suggest the possibility that they may inhibit water absorption.

Observations indicated that *Triturus* does not exhibit any particular specialized behavior related to the conservation of its body water and appears to depend primarily upon its thickened skin and secondarily upon its ventral surface being in contact with the substratum. *Aneides* responds to unfavorably dry conditions by coiling its body and keeping its ventral surface in close contact with the substratum, thus materially reducing the amount of body surface exposed to the air. Its habit of resting close to the substratum facilitates water absorption through the thin and highly vascularized skin of the ventral surface. These behavioral traits enable *Aneides* to retard the loss of water and to replace a water deficit quickly. *Ensatina* also has a highly vascularized skin and, like the other two salamanders, usually keeps its body in close contact with the substratum. However, it seems to be least able to cope successfully with drying conditions. It is generally the

first to retire from the ground surface with the advent of dry weather. Because its surface activity appears to be largely restricted to the rainy season it may, therefore, be subjected to unfavorable conditions of excess moisture. When this is the case, *Ensatina* may behave in a manner that would retard absorption of water—adjusting to the excess by stiffening the legs and raising the body off the ground.

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FROST ACTION AS A PRIMARY PHYSICAL FACTOR IN TUNDRA PLANT COMMUNITIES[1]

ROBERT S. SIGAFOOS

Alaska Terrain and Permafrost Section, U. S. Geological Survey, Washington, D. C.

INTRODUCTION

Some studies in plant geography have shown that the length of time that land surfaces have been exposed to plant colonization is important in the development of vegetation. Raup (1946: 63–64, 75–78) showed that certain types of forest in the Athabaska-Great Slave Lake Region can be correlated with the age of the surface—the length of time that the surface has been exposed to colonization by plants. Fernald's (1925) and Hulten's (1937) classical studies are based on the correlation between glacial and post-glacial history of the species and the age of the land surface. Porsild (1939: 162) suggests that the difference in the vegetation and flora above 1,500 feet in the Nome, Alaska, region from that in the lowlands may be due to persistence of plants on higher, thus older, surfaces while plants at lower elevations were destroyed by submergence of land. Later, Porsild (1951: 12) states that vegetation in the glaciated parts of North American arctic is young and plant communities are unstable, whereas a "climax" may have been reached in nonglaciated parts of arctic Alaska. An excellent discussion is presented by Raup (1951: 105–107) in which he shows that the concepts of physiographic ecology are largely based on ideas of soil stability in vegetation and that because of this stability vegetation has had time to develop. Frost action in soils in tundra regions, however, eliminates the importance of long periods of time in the development of tundra vegetation. The uniformity of tundra vegetation over long slopes modified by intensive frost action and mass movement of soil is pointed out by Raup (1951: 112) as evidence of the primary importance of frost action upon vegetation development. Tundra plant communities can be better correlated with the intensity and character of frost action than with the age of surface. Benninghoff (1952: 42) states that vegetation growing on soils affected by intensive frost action should be studied on the basis of the physical environment.

The ultimate limit of vegetation development is controlled in the final analysis by the length of time during which environmental factors do not fluctuate beyond the limits of the ecological amplitude of the species. In tundra regions, environmental factors frequently and periodically fluctuate beyond the limits of the ecological amplitude of the species. Frost action in soil (congeliturbation), because its intensity fluctuates widely and frequently, is the most important factor in the development of tundra plant communities. Vegetational change is thereby initiated and diverted. The length of time involved in the destruction of vegetation by frost action and its subsequent regeneration is considerably shorter than is the time involved for other environmental changes. Climate in tundra regions has changed; glaciation and other geologic processes have periodically exposed new land surfaces to plant colonization so that many different surfaces now exist that have been exposed for varying periods of time. Frost action is so frequent and effective, however, that it eliminates or submerges the effects of slow, long range climatic changes and the effects of different lengths of time that surfaces have been exposed.

Frost action maintains an unstable substratum in which plants are rooted or upon which they rest. Frequent soil

[1] Based on a paper read at Alaska Science Conference symposium on the "Relationship of vegetation to the physical environment," Nat. Acad. Sci., Nov. 10, 1950. Publication authorized by the Director, U. S. Geological Survey.

movement prevents the development of a true biological succession (Phillips 1934: 562) and the achievement of a climax in even the most liberal sense (Cain 1947: 193). Although detailed field studies were confined to Seward Peninsula, Alaska, there is every indication that frost action exerts an equally profound effect over most of the treeless arctic.

Frost Action

All land surfaces in tundra regions including glacial deposits are subject to frost action, the most effective process of sub-aerial erosion in cold climates. Ice formation in bedding planes and joints in bedrock and within the interstices of the mineral grains breaks the rock into fine particles. Ice formation in the soil results in heaving and thrusting of unconsolidated materials and aids in their downslope movement. The mechanism of frost action on Seward Peninsula has been summarized by Hopkins and Sigafoos (1951) and by Sigafoos and Hopkins (1952).

Frost action creates new surfaces largely by aiding in moving soil masses downslope and also eliminates the effect of differences in the time that the surfaces have been exposed, primarily by periodic stirring. This latter effect will be discussed in detail.

Relationship of Vegetation to Age and Stability of Surface

By simplification, in a glaciated region near Nome, Alaska, four surfaces of different age can be defined. The surfaces are, from youngest to oldest: (1) flood plain alluvium, (2) younger glacial de-

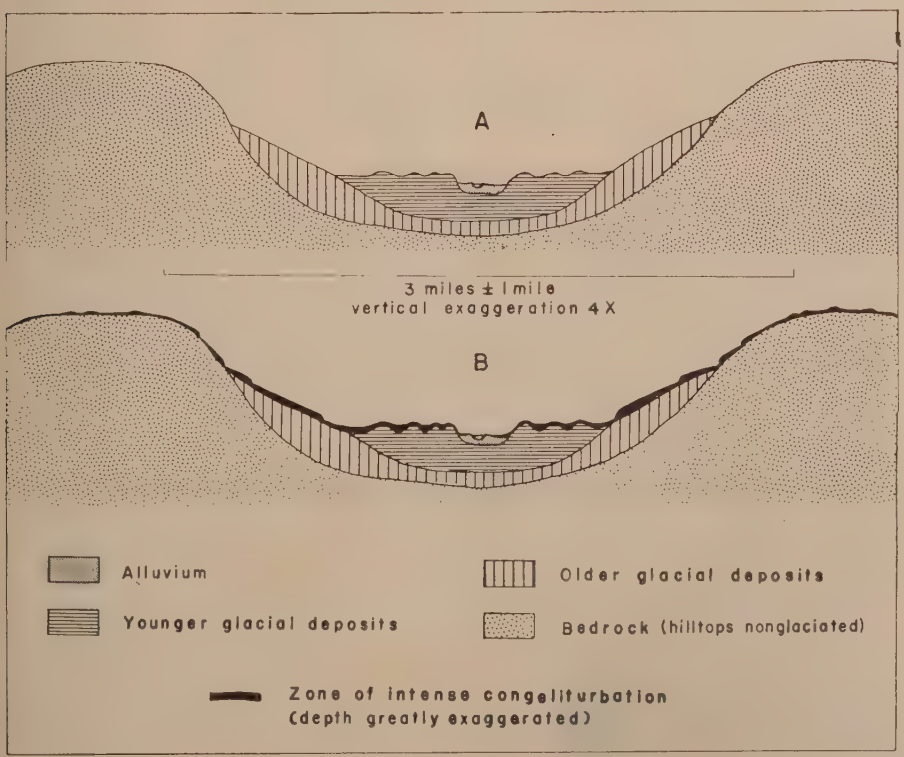

Fig. 1. Diagrammatic cross-sections of a glaciated valley. A. Section showing parent materials and surfaces of different ages. B. Section of valley showing thin veneer of intense frost action which eliminates effects of different ages of surface.

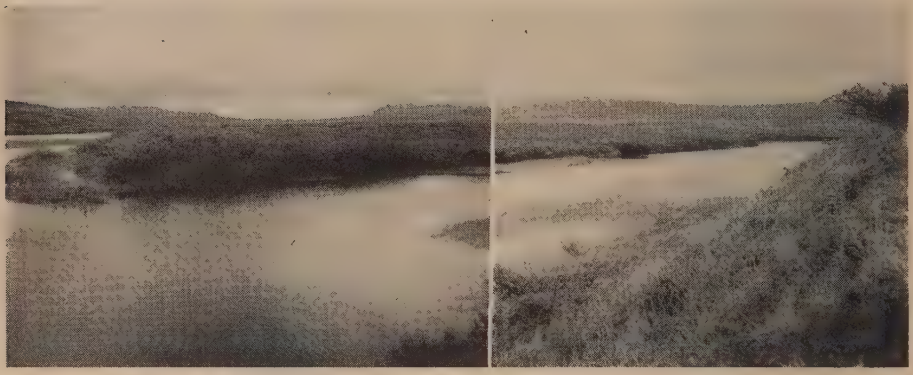

FIG. 2. Panorama of glaciated Nome River Valley. Flood plain alluvium is in middle foreground; glacial till of older glaciation is in far right foreground, in extreme left horizon, and forms floor of broad valley in left distance; nonglaciated surfaces form horizon in left distance. Younger glacial deposits are not visible in this photograph.

posits, (3) older glacial deposits, and (4) higher, nonglaciated surfaces (Figs. 1, 2).

Prominent types of tundra vegetation

Upon these surfaces grow a few hundred species more or less sorted into plant communities, of which only the most easily defined will be discussed. Problems of classification of such arctic plant communities have been thoroughly discussed by Griggs (1934: 155–157) and Raup (1941: 212–214, 1947: 49–50). It would be an almost endless task to describe completely all the vegetation of even a major part of Seward Peninsula.

The communities that will be used as examples of the effects of frost action upon vegetation can be classified according to the drainage conditions of the substratum in which they grow and upon which they rest.

Heath and Dryas mats.—Summits and steep slopes of hills, composed of non-calcareous rock and deposits of coarse materials derived from similar rock, support a community of matted heath and heath-like plants which Porsild (1951: 13–16) classified as a community of unstable screes. *Salix phlebophylla,*[2] *Vaccinium uliginosum* var. *alpinum, V. vitis-idaea* ssp. *minus, Loiseleuria procumbens,* and *Empetrum nigrum* are prominent.

Individual plants usually occur as isolated mats extending only 1 to 3 inches above the substratum. On such summits and steep slopes, nearly 50 percent of the surface is covered with rubble; among the rocks are shallow pockets of silt and humus in which the plants are rooted. The taller woody plants extend a few inches above the substratum to the general level of the boulders. Scattered grasses may reach a height of 6 to 12 inches. Crustose lichens are abundant on the larger rocks and fruticose lichens among the woody plants.

Similar vegetation grows on well-drained gravel knolls of recent glacial moraines and on well-drained gravel terraces.

Well-drained silty and gravelly soils derived from calcareous bedrock support a complex and diversified community of plants in which *Dryas octopetala,* in the broad sense, is the most prominent species. This community is called a rock desert by Porsild (1951: 13). With it grow *Silene acaulis, Carex glacialis, Saxifraga oppositifolia,* and many others.

Communities of these species growing on slopes composed largely of small rock fragments consist of scattered mats of *Dryas* around and in which the other spe-

[2] Nomenclature used follows that of Hultén (1941–1950).

cies are rooted. The environment is extremely unstable, and the *Dryas* mats act as miniature dams against downslope movement of rock. The mats are held in place by a few strong underground *Dryas* stems that extend upslope.

The *Dryas* community that grows on shallow fine-grained soils derived from calcareous rocks on nearly level surfaces forms an almost complete cover in which there appears to be some interdependence among the plants. *Dryas* mat communities also occur on summits and upper slopes of hills of calcareous rock throughout the area and on some recent glacial deposits.

Heath and *Dryas* mats reach their best development in areas of intense frost-riving of rock, and in areas of minor frost-heaving of soil. These mats grow also on gravel deposits and are rooted in pockets of fine soil materials on well-drained summits and slopes. Movement of soil is small because little water is available for ice formation. Small, well-drained areas underlain by calcareous rock where only a 1- to 3-inch soil layer has accumulated are nearly 90 percent covered with *Dryas* mat vegetation. Surfaces underlain by one or more feet of rock fragments and silt are only 5 to 10 percent covered with plants. Intense frost action in the deeper soil prevents the development of a denser vegetation (Fig. 3). Coarse-textured glacial deposits and stream terraces composed of calcareous rock fragments and silt support similarly scanty vegetation. On 20° to 30° slopes of calcareous bedrock hills, plant cover is about 5 percent. Movement of rock fragments destroys the plant and retards growth and germination. Heath and *Dryas* mats occur on nonglaciated surfaces near Nome, and on both the older and younger glacial deposits. Continuous heath and *Dryas* mats, then, indicate frost action of less intensity because of well-drained soil and are not characteristic of surfaces of varying age. Discontinuous mats indicate intense frost action and they, too, are not characteristic of surfaces of different ages.

Willow-birch-heath. — Willow-birch-

FIG. 3. Dark mats of *Dryas* on slope composed of 1 or more feet of small rock fragments and silt. Nearly parallel light bands and darker elongate spots are rock and soil stripes, respectively; these are evidence of frost action on gentle slopes.

heath is a rather loosely defined shrubby grouping of *Salix pulchra, S. richardsonii, Betula nana* ssp. *exilis,* possibly *Betula glandulosa,* and *Vaccinium uliginosum* growing on well-drained soils. The community consists of an open stand of shrubs 3 to 8 feet tall with much open ground among the plants. In the open ground are grasses, sedges, and other herbaceous plants. Willows are not always present, nor are birches or heath; the common characteristics are the open stand and well-drained soil.

Willow-birch-heath grows on frost-derived rubbly soil and well-drained glacial deposits of both glaciations. Frost action is slight at sites supporting willow-birch-heath but is still more intense than at sites where nearly continuous heath and *Dryas* mats grow. Soils supporting willow-birch-heath are well-drained, fine-grained materials 5 or more feet thick. The soil that freezes in winter thaws rapidly to depths of 3 to 6 feet by the end of summer. Little water is available during autumn freezing for the formation of segregated ice masses, thus movement by frost action is slight. The fine-grained soils form gentle slopes, so downslope movement is slight. Movement that does occur is somewhat inhibited by the growth of roots and underground stems of the shrubs.

Cottongrass tussock-birch-heath.—Cottongrass (*Eriophorum vaginatum* ssp. *spissum*) tussock-birch-heath vegetation is one of the few tundra communities in which there exists an interdependence among the plants. The development of this community has been described by Hopkins and Sigafoos (1951: 87–92).

Cottongrass tussock-birch-heath grows on poorly drained silty soils of level or gently sloping surfaces that vary in age from old pre-glacial surfaces to those formed by the most recent glaciation; it grows in only a few scattered areas in the entire glaciated region. Elsewhere on Seward Peninsula, however, it is widespread, being the primary vegetation in at least 5,000 square miles. This community is classified by Porsild (1951: 12–17) as dwarf-shrub heath tundra and he implied that it is climax. Frost action at sites of this community is intense and periods of soil movement occur annually. The characteristic form of microrelief features and of some plants results from the interaction of plant growth and frost action. On level surfaces and slopes up to 3° the plants form circular and reticulate patterns. On 4° to 5° slopes the patterns are elongate downslope.

Circular bare areas develop in tussock-birch-heath vegetation across which the intensity of small scale frost action varies, permitting the initiation of growth of different species. The continued disturbance of the substratum and the destruction and development of vegetation comprise a dynamic, continuous cycle in the physical environment of the community. Recent geomorphic studies indicate that the ultimate in the development of tundra land surfaces is a surface underlain by as much as 10 feet of poorly drained silt over broad areas of hill slopes and stream interfluves (Hopkins, personal communication, 1950). Cottongrass tussock-birch-heath vegetation would grow on this silt. Its development, however, is not dependent upon age of the surface, because it is prominent on ground moraines of the younger and older glaciations near Nome, as well as on still older, nonglaciated surfaces throughout Seward Peninsula.

Sedge sod and willow shrub.—A tight sod of *Carex aquatilis* and *Eriophorum angustifolium* covers poorly defined drainage lines on nearly all gentle slopes. Dense thickets of *Salix pulchra* grow on banks and in channels of drainage lines at lower elevations of higher hills. Sedge sod also grows in level, poorly drained, boggy areas where water stands about the base of the plants throughout the summer.

Peat underlies the sedge sod and willow thickets in drainage lines in bogs. The peat and the deeper soil underlying some drainage lines are not perennially frozen; but where they are perennially frozen, thawing occurs to depths of 3 to 6 feet

by September. Low banks of the channels supporting willow thickets are composed of silty soil, perennially frozen from depths of 3 to 6 feet. Downslope movement of the sod apparently proceeds slowly, forming low transverse ridges upon which more mesophytic species grow. Such extremely wet drainage channels would be common on slopes of the ultimate landscape developed under cold climates. Sedge sod would be conspicuous at these sites and would be a community associated with cotton grass tussock-birch-heath vegetation.

Sedge-filled drainage lines and boggy areas occur on surfaces of all ages. Sedge bogs have developed on surfaces above and below "second beach" at Nome which was formed in deposits believed to be of glacial origin (Mertie 1943: 71). Sedge sod is continuous from the higher to the lower surface in drainage lines extending down the conspicuous escarpment. Similar vegetation occurs throughout nonglaciated areas of the peninsula, in poorly drained saddles on the higher, nonglaciated hills near Nome, on ground moraines of the younger and older glaciations, and within cirques of the most recent glaciation. Detailed examination of this community at these sites has failed to reveal any characteristic form or any species unique to stands on older or younger surfaces.

Correlation of Vegetation with Environmental Factors

It is apparent that the communities described here cannot be correlated with varying lengths of time that surfaces have been exposed to colonization by plants. Other environmental factors have been examined, but frost action in soil remains the most conspicuous factor with which different communities can be correlated.

Variation in environmental factors

Microclimatic and edaphic factors.— Rather detailed microclimatic observations were made in the low hills north of Nome over a period of four months, from July to November, in 1949. They consisted of reading Weather Bureau type maximum and minimum thermometers every other day at about 25 stations, of recording continuous air temperature at about 6 stations on thermographs, and of recording continuous soil temperatures at a 6-inch depth with mercury-actuated recording thermometers at three stations. The stations were concentrated around a small hill with a relief of approximately 900 feet and an area of about one-half square mile. Other stations were located on the coastal plain near Nome and in the lowland of the Nome River, 10 miles to the northeast.

The briefly analyzed studies show that only minor and expected variations in microclimates are consistent between widely separated stations. They show that north-facing slopes are colder than south-facing slopes. Clouds and fog narrow the range between maximum and minimum air temperatures; stations covered with low clouds or fog coming from Bering Sea experienced narrower temperature ranges than stations farther inland, where the sky remained clear. Within the area of a small valley, variations in microclimates were found to exist but none of the variations were consistent.

All the plant communities previously described occur in the microclimatic study area. It has not been possible to correlate the communities with any variations found in microclimates. Perhaps climatic factors cannot be measured by present methods with the accuracy necessary to make such correlations.

Other environmental factors were investigated. Acidity of soil was measured by small field testing kits. Large variation was noted but, again, no correlations could be made with different communities. Soil pH varied from 4 to 8 under *Dryas* mats and from 4 to 6.5 under heath mats, depending upon the quantity of humus in the sample. Some factor in

well-drained, thin soils related to calcareous rocks as against siliceous rocks, such as pH or calcium, probably is effective in determining whether the community is *Dryas* mat or heath mat assuming that species of each community are available for colonization. Kind and intensity of frost action, however, seem to determine the degree of continuity of the plant cover in each community. Whether or not the vegetation is a heath mat, willow-birch-heath shrub, or cottongrass tussock-birch-heath vegetation is again determined by the kind and intensity of frost action in the soil.

Soil samples were collected to determine variation in soil moisture content under varying climatic conditions and under different site characteristics. It was found that because of the difficulty of obtaining uniform samples, the percentages of water obtained were largely meaningless. Under a heath mat, the percentage of moisture varied from 59% to 125% of the dry weight of soil; the wetter soil contained an appreciably greater amount of humus. Mineral soil under a type of vegetation not described here, *Dryas-Cassiope-Empetrum* mat, contained 23% to 27% water; the overlying peat contained, at the same time, as much as 230% of the dry weight as water. Although these figures show that more water is present in areas where considerable peat has accumulated, it must not be inferred that frost action is greater here than in areas where peat is lacking and soil is drier. Peat effectively insulates the ground, so that freezing and thawing occur less frequently, and peat, especially when frozen, offers great resistance to heaving by ice formation.

Frost action.—Frost action is a process whose intensity depends upon the interaction of all elements of the environment. The intensity of the process can be measured only by continued observations under specialized conditions. Microrelief features formed by frost action, however, can be observed; and the distribution of them can be correlated with the distribution of plant communities.

Conclusions

Microrelief features and variations of intensity and character of frost action extend across the glacio-fluvial deposits with little difference from one deposit to another (Fig. 1B). Vegetation that is in equilibrium with the different frost-formed deposits follows them across the glacio-fluvial deposits. D. M. Hopkins studied the deposits in the Nome River area and in order to map them he found it necessary to examine all available exposures, and to make exposures where none existed. He could not use variations in vegetation as boundaries between surficial deposits of different origin. The age of the youngest glacial deposits must be of the magnitude of several thousands of years. Age of the microrelief features is measured in decades, or a few centuries at most. The frequency of intense frost action eliminates to a large extent any effects that varying lengths of time that surfaces have been exposed to plant colonization may have had upon the development of vegetation in tundra regions.

How widespread the area is in which frost action is or has been a prominent physical factor in the plant environment is not completely known. It is the primary agent of subaerial denudation in tundra regions; it is less active but still effective under spruce near its arctic limit. It is not limited to areas underlain by a perennially frozen substratum. At the Alaska Science Conference of 1950, W. S. Benninghoff described active frost action on Kenai Peninsula. Denny (1940) has found active miniature stone rings in New Hampshire. The interaction of frost action and plant growth in low latitudes has been described by others (Sigafoos and Hopkins 1951). Frost action and mass movement were effective in modifying middle-latitude land surfaces during advances of Pleistocene ice (Smith 1949: 1497–1503). Throughout the North

American continent, at least as far south as 40° North latitude in the midwest, frost action has varied in intensity throughout the time our present vegetation has been developing. It is necessary to assume that a vegetation cover similar at least in form to that in present day tundra regions was present in peri-glacial regions in order to explain the presently inactive frost formed deposits.

Summary

Although age of the surface may be important in the development of vegetation in some regions, its effects are largely eliminated by frequent and intense frost action in the tundra of Alaska. Surfaces that have been exposed for varying periods of time—surfaces recently formed by water and glacial ice—are essentially of the same age because periodic stirring of the surface layers continually exposes new surfaces to plant colonization.

Four distinct types of vegetation: heath-*Dryas* mats, willow-birch-heath, cottongrass tussock-birch-heath, and sedge sod and willow shrub, occur on three surfaces of varying age (younger glacial till, older glacial till, and unglaciated surfaces). Willow-birch-heath and sedge sod and willow shrub also grow on flood plain alluvium. The distribution of these types of vegetation can be correlated with different types of microrelief features that are formed by frost action. Their distribution could not be correlated with other environmental factors that were investigated.

The effect of frost action upon vegetation is not limited to regions of perennially frozen ground. Frost action is effective in lower latitudes at the present time and has been more effective in the past.

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SYLVATIC PLAGUE STUDIES, IX. STUDIES OF THE MICROCLIMATE OF THE CALIFORNIA GROUND SQUIRREL BURROW AND ITS RELATION TO SEASONAL CHANGES IN THE FLEA POPULATION [1]

D. S. Longanecker and A. L. Burroughs [2]

George Williams Hooper Foundation, University of California, San Francisco 22, California

This study was instituted to learn more about the environment of fleas that infest the California ground squirrel *Citellus beecheyi* (Richardson). Two primary objectives were: (1) to study the relationship of burrow temperature to flea infestations of the squirrels and (2) to learn the temperatures that fleas of this important rodent reservoir of sylvatic plague are naturally exposed to during the immature stages of their life cycle and while they are off the host during their adult stage. *Citellus beecheyi* was chosen for the study because of its well-demonstrated importance in the maintenance of plague in the western part of the United States.

The microclimate of rodent burrows has been studied before, but usually the principal interest in the studies was not centered on the influence of these conditions on flea populations. The microclimate of the kangaroo rat in the hot, dry Arizona desert during the hottest season (Schmidt Nielsen and Schmidt Nielsen 1950) and of several desert animals in southwestern United States (Vorhies 1945) and the temperatures of gerbil burrows in the sandy semi-desert between the lower parts of the Volga and Ural Rivers (Rall 1939) have been described. Storer (1933) gave the dimensions of some burrows in California and described the colonial systems, and Linsdale (1946), in his excellent work on the natural history of this squirrel, discussed at some length the dens and their construction and use by the squirrel.

Ecologic studies of squirrel fleas have been made by others. The most relevant to the study being reported are the temperature observations of Stewart and Evans (1941) on *Hoplopsyllus anomalus* (Baker) 1904, predominant on *Citellus beecheyi* in central California during the hottest season, and *Diamanus montanus* (Baker) 1895, predominant during cooler seasons. The fleas they studied were at the entrances of the burrows and from trapped squirrels, and the temperatures they recorded were taken 1 foot within the mouth of the burrow and 6 feet above ground. Their work was done in the same area as that in the present study. Ioff (1941) also observed that the populations of ground squirrel fleas change annually, that the majority live only for 3 to 5 months, and that at different seasons different species prevail.

The work to be described was done at the field station for ecologic studies of the George Williams Hooper Foundation, University of California. The site of this study area is Calaveras Dam on the border of Alameda and Santa Clara Counties in central California. For a detailed description of this region, see the paper by Evans and Holdenried (1943).

Materials and Methods

In preliminary unsuccessful attempts to record burrow temperatures at Calaveras Dam, resistance thermometers were tied to squirrels released at burrow entrances. Frequently the units were torn from the leads because the wire caught on rocks and other obstructions in the

[1] Aided by grants from the Rosenberg Foundation.

[2] Present address: U. S. Public Health Service, Communicable Disease Center, Atlanta, Georgia.

burrows. Sometimes squirrels stopped just inside the burrow and occasionally they gnawed the coil and leads loose and broke the circuit. Moreover, it was never certain how much the body temperature of the squirrel affected the reading. It seemed more reliable to us to push the thermometers into the burrows by hand. The Schmidt Nielsens (1950) used both methods—they introduced Krogh's microclimate recorders, tying the instrument to the animal's tail so that the animal pulled it 3 to 4 meters into the burrow or they pushed the instrument about 1 meter into the burrow at the end of a stiff wire.

In the present studies, temperatures were measured with resistance thermometers. Five Leeds and Northrop nickel thermohms with a limit of error of 0.5° F. and a change of resistance of 18.63 ohms between 0° and 100° F. were used. A resistance reading was obtained and converted to degrees Fahrenheit with the aid of Standard Conversion Tables for Leeds and Northrop thermohms. In addition, four copper-wire resistance coils were constructed in the laboratory. They were calibrated by plotting the resistance at $-0.5°$ and 30° C.—a straight line relationship. Any resistance reading could be converted directly to temperature by consulting the graph. The resistance of the coils and thermohms were measured with a Leeds and Northrop testing set (no. 5300), basically a Wheatstone bridge. Figure 1 shows the testing set hooked up to the lead-covered three-conductor cable leading to a coil in burrow system 1.

Three burrow systems were studied: one artificial and two natural burrows. In the natural burrows, resistance thermometers were inserted as far into the burrow as they could be pushed.

Artificial burrow. This burrow, made of red tile drain pipes 5 inches in diameter, was constructed in an open space shaded a little by oak trees to the south during the winter. It was built on the east side of Calaveras Creek Canyon, a little above the level of the top of the dam. Figure 2 is a view of the location. It slopes about 10 degrees to the west. The ground was covered by various grasses in normal density over the burrow in the spring when studies were started. This location is near some old excavations, the dirt from which had been used in the con-

FIG. 1. Testing set attached to thermometer no. 26.

FIG. 2. Area surrounding artificial burrow. The burrow is to the right of the row of fence posts, upper left.

struction of the dam. The distance from the burrow to the nearest edge of the excavation was 14 feet. The site was chosen primarily because there were squirrel burrows on it. These were used by squirrels periodically, but were not in use at the time the studies were undertaken.

The artificial burrow, constructed in the autumn of the year preceding that in which temperature recordings were begun, was made by burying the unglazed terra cotta pipe in a trench. The north tube was laid on rocks (f) to allow rain water drainage. During construction a chamber (a) was hollowed out of the earth, forming an extension of the tube (b) (Fig. 3).

In early June a thermohm was installed

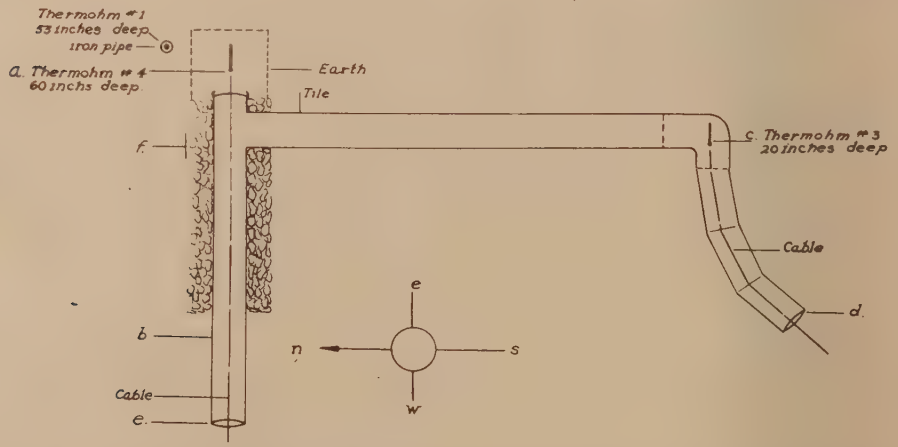

FIG. 3. Top view of artificial squirrel burrow, made of tile drainage pipe. Depth is in inches below the surface of the earth; *a*, cavity 60 inches below surface thermohm no. 4; *b*, north tube; *c*, thermohm no. 3, 20 inches below surface; *d*, south entrance; *e*, north entrance; *f*, rocks under north tube.

FIG. 4. Area surrounding burrow system 1. Burrow is just below the lowest road, below the dam.

on the bottom of the cavity (a), about 5 feet deep. The north tube (b) was closed off loosely with rocks (at (e)) to prevent undue ventilation. A thermohm (c) was also installed at the south entrance (d) at a depth of 20 inches. This entrance was left open. It is not known if a squirrel ever entered the artificial burrow, but once the head and neck of a large gopher snake was seen in the mouth of the burrow. When the thermohms were permanently removed, wood rat fecal pellets were found in the south entrance (d) and the north tube (b) and the lead cable of the thermohm at the bottom of the cavity (a) was urine stained. Nests were not found in the artificial burrow.

Burrow system 1. This system was located on the east side of the canyon below the dam (Fig. 4). Two resistance

FIG. 5. Area surrounding burrow system 2. Burrow is in the center of the picture.

thermometers were introduced into this burrow in July and removed in September of the following year. The first, 30 inches from the mouth of the burrow, was partially buried in the sand at a vertical depth from the surface of 13 inches. The second was placed 6 feet from the mouth of the burrow and 15 feet south of the first. It was approximately 42 inches from the nearest surface. When this thermometer was dug up, 1½ feet of the burrow in front of it was found to be plugged with damp sand. There were signs that squirrels occasionally entered this burrow, and fleas were seen several times at the entrance. The texture of the sand was loose so the thermometers were probably always buried by it.

Burrow system 2. Early in June a thermohm was pushed about 8 feet into the natural burrow. It was probably in close contact with the soil on the floor of the burrow about 30 inches from the cut surface of the road bank. About the same time a resistance coil was pushed 2½ feet back into a burrow some 9 feet to the left and below the thermohm. It was about 18 inches in from the surface of the road cut (Fig. 5) on a west-facing slope a quarter of a mile west of the dam. At this time the burrow entrance was full of dry *Bromus* seeds, indicating that it was inactive. The following March the burrow seemed to be uninhabited, but by the middle of the following June it had been plugged with soil from the inside and the coil was securely buried. When this coil was eventually dug out, the soil around it was damp yellow clay and sand.

Soil temperatures. In July a thermohm was placed 53 inches below the surface in a two-inch iron pipe pounded into the ground. The pipe unit was about a foot north of the cavity of the artificial burrow, and the readings obtained in it are considered soil temperatures. A second

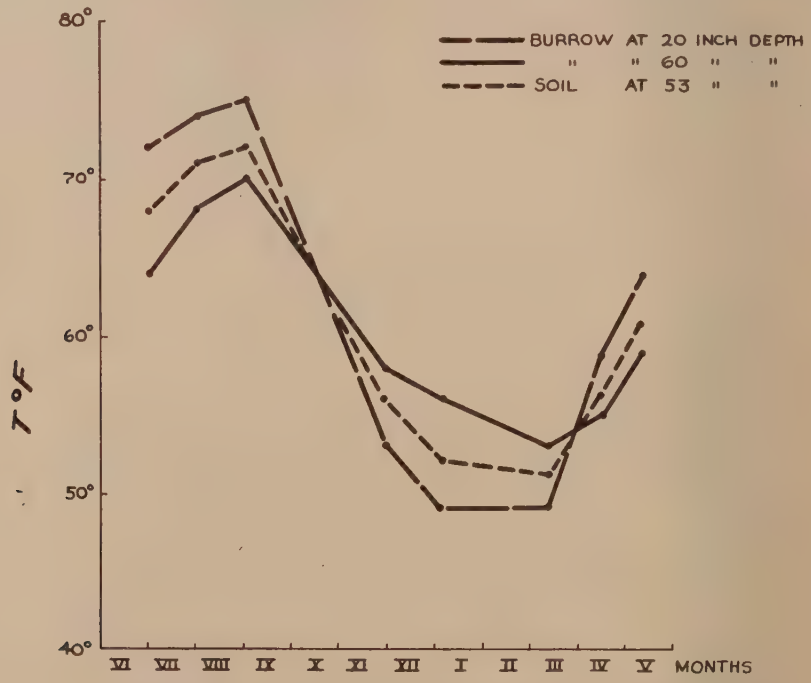

Fig. 6. Artificial burrow and soil 1 foot from the burrow. Mean 48-hour temperatures measured periodically.

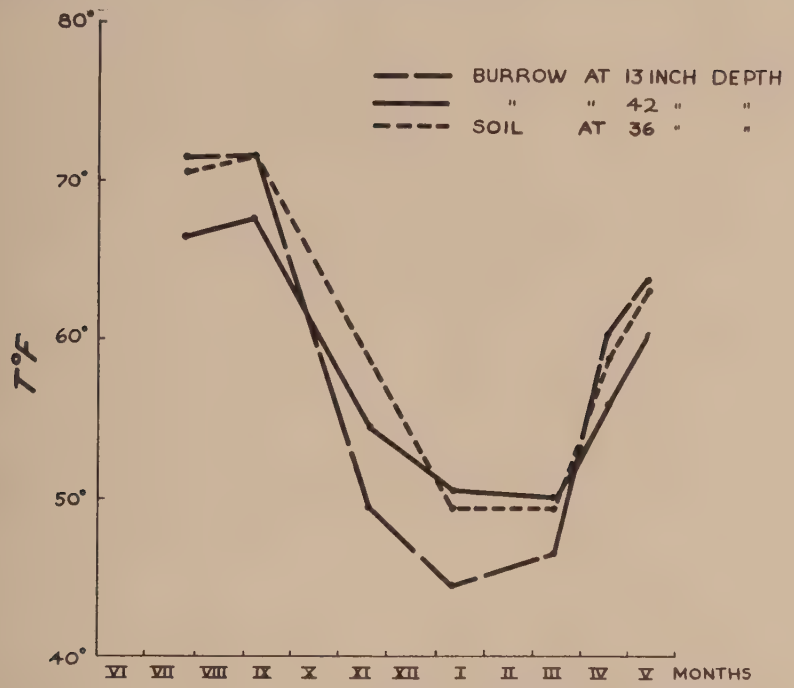

FIG. 7. Burrow system no. 1. Mean 48-hour temperatures measured periodically.

pipe was driven into the sand to a depth of about 36 inches near burrow system 1. A resistance thermometer was placed at the bottom of the pipe.

Humidity readings. A few relative humidity readings were taken in burrow entrances in August and September. These data were desirable because fleas often are found in the mouths of burrows in great numbers. Wet- and dry-bulb readings were obtained a distance of some few inches inside the burrow by using the Gray (1929) cog psychrometer. It is realized that this apparatus is not the most desirable for obtaining relative humidity readings because the gear ratio of the mechanical apparatus and the circumference of the thermometer swing are such as to make it impossible to pass the required 15 feet of air per second over the wet-bulb thermometer, the conditions for which the humidity tables are calculated. However, when checked against a sling psychrometer, the readings agreed within 3 to 6 per cent relative humidity.

Collection of fleas. Fleas were collected from the burrow entrances by placing a white flannel cloth in the burrow entrance and then transferring it to an enamelware pan and removing the fleas from the pan with an aspirator.

Observations and Discussion

Figures 6 to 8 are periodic records of temperatures in the 3 burrows. Each point represents an average of readings taken about every 2 hours for 48 hours. The variations in temperature in the 3 burrow systems are similar and of the same magnitude, but most of the temperatures in burrow system 1 are slightly lower than those of the artificial burrow, possibly because burrow system 1 was located where there is less direct sunshine and where it is a little cooler in the morning.

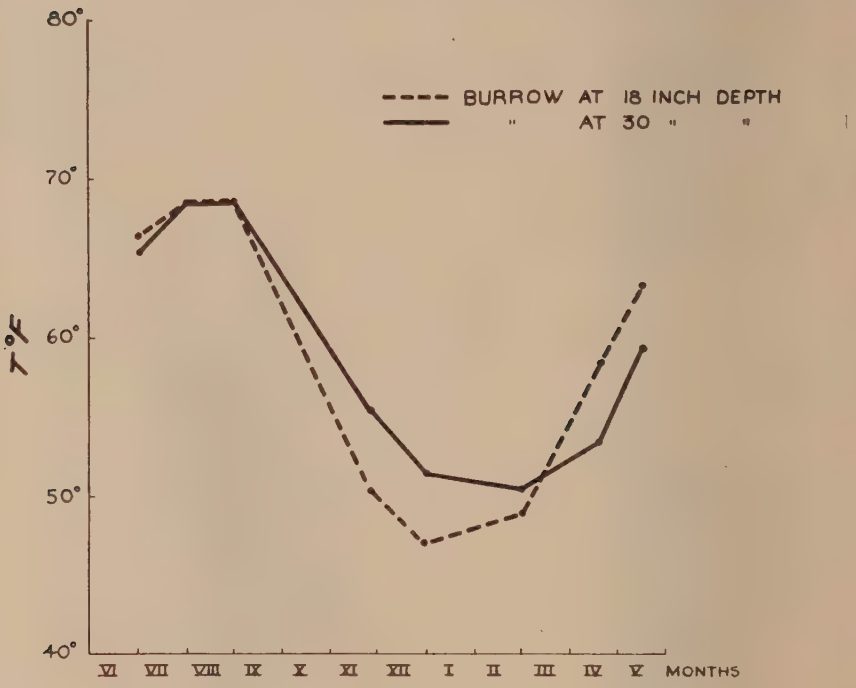

FIG. 8. Burrow system no. 2. Mean 48-hour temperatures measured periodically.

The maximum temperature recording in any single 48-hour period was made the last of August and the first of September in the artificial burrow. At the 20-inch depth a maximum reading of 77° F. was obtained at 4 o'clock in the afternoon, and a minimum of 74° F. was recorded in the early morning hours and lasted until 9:30 to 10 A.M. At the 60-inch depth the temperature was highest (71° F.) at 6:30 P.M. and lowest (69° F.) between 5 and 7 A.M. During this entire period the soil temperature at 63 inches remained a constant 72° F.

The minimum temperature recordings in the artificial burrow were obtained during the period of March 8 to 10, 1945. At the 20-inch depth the lowest temperature was 49° F., at the 53-inch depth, 51° F., and at the 60-inch depth, 53° F. During this period the temperature at the 53-inch depth increased less than 1°.

The greatest variation in temperature in any 48-hour period was recorded the last of June at the 20-inch depth. At that time the temperature ranged from 70° to 76° F., with a mean of 72° F. Other readings for all depths were either constant or varied only 1° to 3°.

The depths of 4 ground squirrel nests in the area of the study plot were all less than 5 feet, though some partially excavated squirrel burrows were as deep as 6 feet 10 inches. In mid-June a predator dug out a burrow and exposed a nest. The top of the nest chamber was 4 to 6 inches, and the bottom was 12 to 14 inches below the surface of the ground. The nest had apparently been occupied; fleas, flea larvae and ticks were collected from it and 100 fleas were collected from the surrounding ground. Early in May, 2 other nests were exposed by a predator. One was 36 inches below the surface of the ground. Some of the grass in it was still green and a few fleas were found. It had evidently been constructed that spring. The other nest was 18 to 24 inches below

TABLE I. *Relative humidity and temperature recordings in burrow entrances*

Date	Burrows sampled	Burrows yielding fleas	Fleas collected	Temperature				Relative humidity			
				Range		Mean		Range		Mean	
				Burrows	Atmosphere	Burrows	Atmosphere	Burrows	Atmosphere	Burrows	Atmosphere
Aug. 10 4–6 P.M.	8	4	92	77–84	78–84	79	81	35–54	32–39	46	35
Aug. 11 10:30–11:30 A.M.	5	1	87	72–84	72–78	76	76	43–57	36–45	51	41
11:30 A.M.–12 M.	4	1	1	78	78–80	78	79	46–49	35–39	47	37
3–6 P.M.	9	6	78	79–86	82–89	84	85	35–50	30–36	43	34
Aug. 12 11–12 A.M.	5	5	68	80–83	75–81	80	80	46–56	43–47	49	45
2–8 P.M.	8	5	121	67–85	71–87	76	78	35–90	35–65	61	48
Aug. 13 6:30– 7:45 A.M.	6	0	0	60–64	57–60	61	58	79–89	83–88	86	86
9:45–11:30 A.M.	8	7	93	70–77	64–73	73	69	56–73	57–80	63	64
7:15– 7:45 P.M.	5	2	13	70–72	65–69	71	68	64–77	59–70	69	64
Aug. 14 6:30–8 A.M.	10	5	22	57–66	54–56	60	54.4	74–95	88–100	87	93
10 A.M.–12 M.	15	6	182	61–76	58–70	68	65	51–89	55–89	68	69
Sept. 15 10–11:30 A.M.	7	3	18	70–76	66–74	72	68	64–66	50–62	65	59
12 M.–2 P.M.	9	6	101	68–72	70–72	70	71	49–80	57–65	65	61

the surface of the ground. A few fleas were found there. The grass in this nest was old; some of it was mildewy. These 3 nests were on the back of the dam.

Another burrow was excavated for study on a slope facing west and a nest was found 4½ feet below the surface of the ground.

The depths of these nests furnish some evidence that the depths of the resistance coils in the artificial burrow were in the same range as nests in active squirrel burrows. Therefore, the temperature data presented probably represent general temperature conditions of unoccupied *Citellus beecheyi* burrows for the area studied.

The soil around the recently excavated nests was moist, and in the burrow system would probably provide a high relative humidity. In many of the burrows the soil was moist up to the mouth and damp earth could easily be reached inside near the entrance. When this moist soil was scooped out with a small digging instrument,[3] many *Ornithodoros parkeri*[4] were found clustered around the mouth of the burrow, probably attracted by the temperature of this location, higher than that in the nest during the summertime. Had the relative humidity not been high, these ticks would probably have desiccated rapidly.

Table I shows that the temperature (measured with a dry-bulb thermometer) inside the burrow, near the entrance, does not vary to any considerable extent from that of the outside atmosphere. The variation is considerably less than can be recorded in the atmosphere between sunlit and shaded places. The mean relative humidity of the burrow entrance is higher in most cases than that of the atmosphere outside the burrow. It would be expected that atmospheric relative humidity would affect the relative humidity in the entrance of the burrow, and it has been shown to do so. However, humidities were maintained approximately 10 per cent higher in the burrow mouths than in the outside atmosphere during periods of decreased atmospheric humidity.

TABLE II. *Air temperature for 48-hour periods*

Period	Maximum	Minimum	Average maximum	Average minimum	Average temperature
VI June 29	96	56			
June 30	94	56	93.3	54	73.6
July 1	90	50			
VII July 30	92	54			
July 31	88	56	87.3	52.7	70
Aug. 1	92	48			
VIII Aug. 31	84	60			
Sept. 1	88	56	86	56	72
Sept. 2	86	52			
XI Nov. 28	54	38	54	38	46
I Jan. 2	48	34	45	33	39
Jan. 4	42	32			
III Mar. 8	64	30			
Mar. 9	66	34	64.7	33.3	49
Mar. 10	64	36			
IV Apr. 19	88	46			
Apr. 20	74	30	81	45.3	64.5
Apr. 21	70	40			
V May 10	78	54			
May 11	80	40	76	47.3	61.7
May 12	70	48			

In the artificial burrow constructed by Vorhies (1945) near *Citellus tereticaudus* burrows at a three-foot vertical depth, the mean maximum temperature was 77° F. and the mean minimum was 72° F. during the week in which readings were made with soil thermograph bulbs. The temperature of the burrow studied by Rall (1939) did not differ by more than 1° C. from that of a corresponding layer of sand. In shallow empty burrows about 60 cm. deep the temperature fluctuated between −2.3° C. in January and 24.6° C. in July. The temperature of the winter burrows about 3 meters deep fluctuated from 7.1° C. in March to 16.7° C. in September.

In the microclimate studies of the

[3] The conventional "tick digger" used by the personnel of the Rocky Mountain Laboratory and others.

[4] Misidentified in a previous study (Holdenried, Evans, and Longanecker 1951) as *Ornithodoros turicata.*

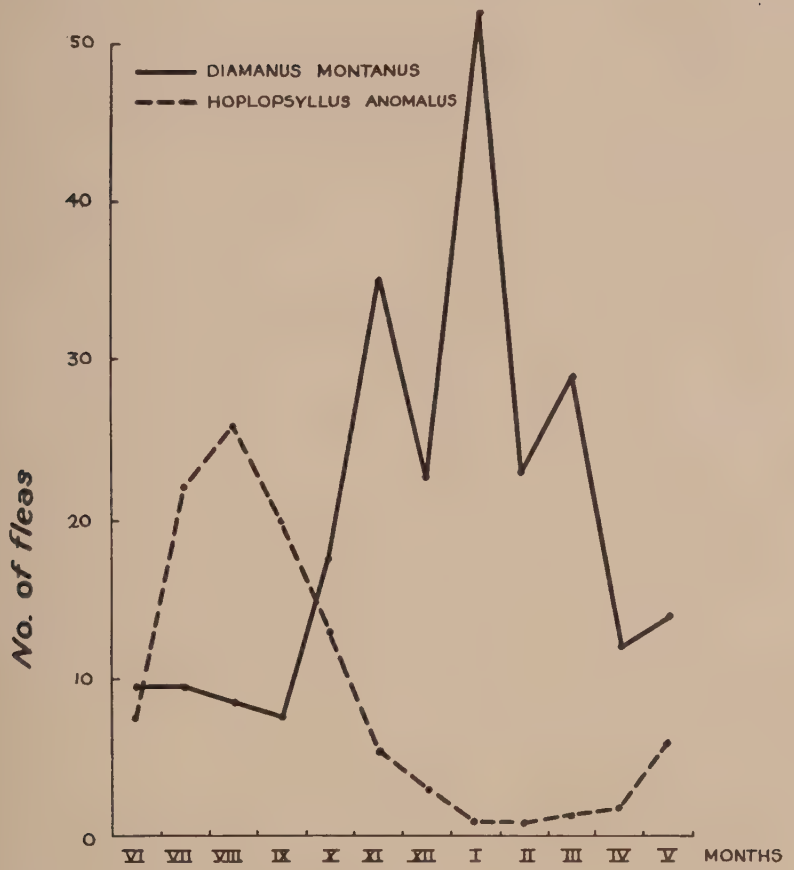

FIG. 9. Seasonal variation in the number of fleas per squirrel (5-year average).

Schmidt Nielsens (1950), made with Krogh's microclimate recorders which record temperature and relative humidity continuously for 12 hours, even during the hottest and most arid season the soil contained enough water to keep a closed air space in the ground at a depth of 30 cm. saturated with water vapor. In the burrows of kangaroo rats the moisture content was two to five times greater than that of the air outside, and the average humidity of the nest chambers was about 30 percent. The burrows were so well ventilated that there was an actual drying out of them. The range of relative humidity in the burrows was about 17 to 62 percent. The temperature ranged from 22.5° to 43.5° C. in these burrows. In the laboratory these rats did not survive for long at temperatures above 38° C., so the Schmidt Nielsens concluded that the holes where the higher temperatures were recorded were probably not the main burrows.

Table II shows the air temperature 5 feet above the ground in the shade of a building near burrow system 1. It is based on readings made with a maximum-minimum thermometer in the same 48-hour periods for which the burrow temperatures were recorded. This table is presented in order to give an idea of the air temperatures in the area at the time the study was made.

During the period of sampling burrows in this area for fleas, 2 burrows yielded

more fleas than any of the others. From one, at five different sampling times, the following numbers of fleas were collected: 87, 88, 91, 167 and 109. Another burrow yielded 31, 51 and 45 fleas on three samplings. There was no correlation of temperature and humidity with the number of fleas collected in the mouths of the burrows.

Figure 9 illustrates the seasonal variation in the number of fleas collected from *Citellus beecheyi* live-trapped in the study area. It is a 5-year average of fleas per squirrel from each of the 12 months. Seasonal variation of burrow temperatures undoubtedly affects the breeding of fleas *Diamanus montanus* was predominant when the average burrow temperatures were below 60° F. at all depths, and *Hoplopsyllus anomalus* was predominant when the average was above 60° F. at all depths. The trends of flea populations for different seasons were similar to those noted by Stewart and Evans (1941)—*H. anomalus* was predominant when the mean air temperature exceeded 75° F. and *D. montanus* was predominant when it was below 75° F. The number of *H. anomalus* on squirrels varies directly with the burrow temperatures; the number of *D. montanus* varies inversely.

Acknowledgment

The authors wish to express their appreciation of the technical assistance of Quentin Tomich and Robert Holdenried in carrying out parts of this study.

Summary

Soil temperatures and temperatures of an artificial burrow and of 2 *Citellus beecheyi* burrows in central California were studied. The depths of the artificial burrow were in the range of depths of at least 4 ground squirrel nests dug out in the area where the study was made. Temperatures were recorded periodically over an approximately 11-month interval by means of resistance thermometers and represent 48-hour averages of recordings made about every 2 hours. Shallow burrows showed the greatest daily and yearly variations in temperature; soil temperatures were the most stable.

Minimum winter and maximum summer readings in the 3 burrow systems and in the soil are:

	Depth, inches	Temperatures (° F.)	
		Minimum	Maximum
Burrow 1	13	44.5	71.5
Burrow 2	18	47	68.5
Artificial burrow	20	49	77
Burrow 2	30	50.5	68.5
Burrow 1	42	50	67.5
Artificial burrow	60	53	71
Soil	36	49.5	71.5
Soil	53	51	72

Temperatures in a burrow measured at 2-hour intervals for 48 hours varied little. The greatest variation, 6° F., occurred in late June at a depth of 20 inches. At 60 inches the temperature readings made on the same schedule were usually constant, but varied 1° in January and in May.

For a brief interval in August and September, temperature and relative humidity recordings were made in several burrow entrances. Temperatures in burrow entrances did not vary greatly from that of the outside air. During periods of decreased atmospheric humidity, burrow entrance relative humidities were about 10 per cent higher than the relative humidity of the outside air.

Populations of the two squirrel fleas, *Diamanus montanus* and *Hoplopsyllus anomalus,* varied with the seasons. The former was predominant when the average burrow temperatures were below 60° F. and the latter when they were above 60° F.

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THE NATURAL DISTRIBUTION OF RED PINE IN NEW YORK

David B. Cook
12 McPherson Terrace, Albany, N. Y.
Ralph H. Smith
New York State Conservation Dept., Albany, N. Y.
and
Earl L. Stone
Agronomy Department, Cornell University, Ithaca, N. Y.

Red or Norway pine (*Pinus resinosa* Aiton)[1] is a tall forest tree, by far the finest member of the hard pine group to be found in the Northeast. It is distinguished from other northeastern members of the genus by its red bark, two long straight needles to a sheath, and egg-shaped cones without prickles on the cone-scales. No experienced observer would ever mistake its identity. The smooth, columnar trunks crowned by heavy, dark green foliage, coupled with a tendency to grow in even-aged groups, give to red pine stands a strikingly handsome appearance, quite unlike anything else in our northern forests. Ecologically, it is a species which exhibits but little variation, especially in the younger age-classes. There is at least some tendency toward the development of local strains. Buell (1940) has pointed out that, in West Virginia, local seed from North Fork Mountain produced better seedlings than did seed brought in from Maine. Eliason (1950) has also reported differences between strains, based on experience in New York.

The natural range of red pine is practically coextensive with the Hemlock-White Pine-Northern Hardwood region of Braun (1950). It extends in a broad band from Manitoba and Minnesota eastward to the St. Lawrence estuary, the coast of New England, and to Newfoundland, with two outliers in the mountains of West Virginia (Buell 1940; Core and Davis 1944). The map of the over-all range (Fig. 1) is largely after Munns (1938), with refinements following Johnston (personal communication 1951) for Ontario, Ibberson (1949) for Pennsylvania, Clausen (1939) for New Jersey, and our own data for New York. We have not attempted a complete revision of the range map. The south boundary of the Wisconsin glaciation is taken from the Glacial Map of North America (Flint 1945).

Within this area, fifteen hundred miles long by five hundred broad, the species varies considerably in abundance and in ecological position. Braun (1950) says that "in the northern tier of counties [in Minnesota] and in adjacent parts of Canada, the climax dominants are Norway (red) pine and white pine, either in mixed or pure stands; . . . . This far north, there are no other species which can compete with the pines." Southward and eastward, and with increasing precipitation, red pine is less abundant, more scattered, and not so frequently dominant. In New York, it sometimes represents a fire disclimax. However, the bare fact that is still occupies substantially the same sites that it did two centuries ago argues strongly for its classification as a climax type on certain well drained locations especially suited to its requirements.

In the western and northern parts of the range, the driests soils are occupied by jack pine (*Pinus banksiana*); in the south and east by pitch pine (*P. rigida*). Red pine prefers the middle ground, be-

[1] Scientific nomenclature follows Fernald (1950).

tween jack and pitch pine on the drier sites and white pine sites where conditions are more mesic. Characteristically, it is a tree of the well-drained but not the droughtiest soils, to which it is well-fitted by virtue of its deep, wide-spreading root system (Adams and Chapman 1941). It appears to be much less adaptable than are the associated white, jack, and pitch pines, which occur over a much wider variety of soil conditions.

With the exception of the outliers in West Virginia, the present range of red pine east of Lake Michigan lies within or closely adjacent to the territory glaciated during the late Pleistocene. Perhaps the West Virginia stations mark the location of an eastern refuge from Wisconsin ice, for they lie some two hundred miles south and east of the limits of farthest glacial advance in this region.

Red pine is a valuable timber tree and, because it can so successfully be established by planting, it has long been a favorite for reforestation. Many millions of seedlings have been set out and many plantations, now grown to seed-bearing age, have begun to reproduce themselves. With the passing of another decade or two, it may be difficult to distinguish with certainty the indigenous stock from the progeny of planted trees of unknown ancestry and uncertain provenance. When that happens, the pattern of natural distribution and all that it means to the phytogeographer, the geneticist, and the ecologist, will be lost forever. This is particularly important in New York because so many red pines have been planted within the state (according to Eliason (1950) 225 million in the past forty years), because seed has been procured

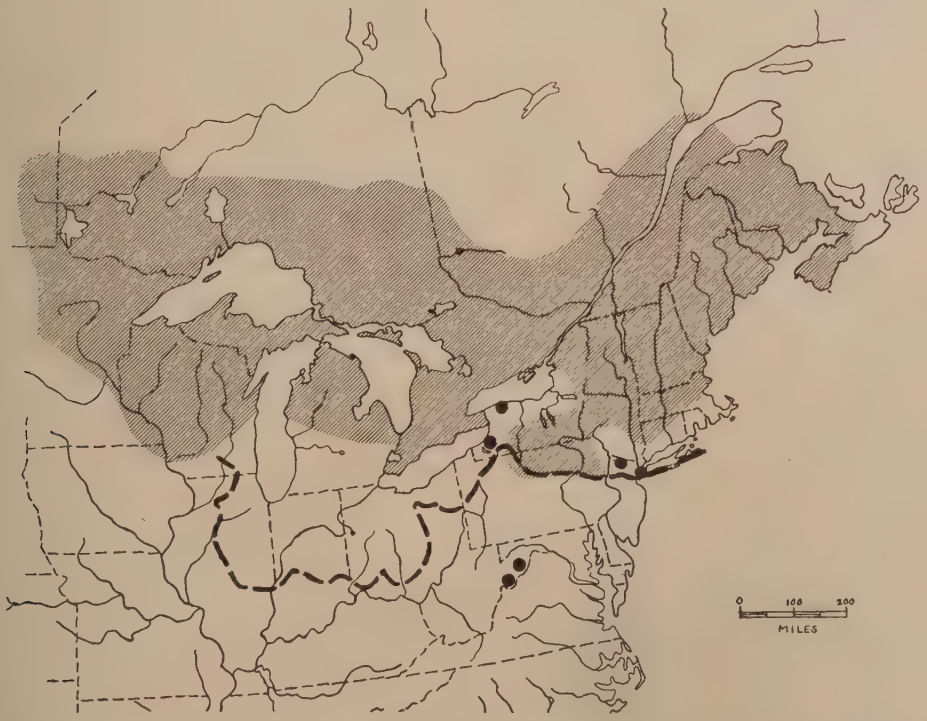

FIG. 1. Natural distribution of red pine on the North American continent, with the southernmost limits of Wisconsin glaciation superimposed.

from numerous locations scattered over most of the natural range, and because the distribution pattern of our native stands is so scattered and discontinuous. Therefore, it seemed imperative to us that we assemble and analyze such data as were available and that we gather such new information as we could, to delineate in detail the past and present natural range and do to determine, if possible, the true nature of the apparent gaps in distribution.

Distribution Records

The earliest records of red pine in New York, that are known to us, date from the middle of the eighteenth century, when white man's occupancy was confined to the main river valleys. Peter Kalm (1750), the Swedish botanist and student of Linnaeus, made a trip on foot and by canoe and sailboat, from Albany to Montreal and back. On his way north, in the spring of 1749, he took the Hudson River –Wood Creek–South Bay route to Crown Point, thence down Lake Champlain. That he reported no red pine is understandable, for none is known along the first part of his journey and the details of the shoreline forest would have been difficult to discern from a sailboat out on the lake, even for such a keen observer as Kalm. The return journey, in October, was by way of Lake Champlain, Lake George and the carry to the Hudson at Glens Falls. Writing from Northwest Bay on Lake George, Kalm reports that "the pine with leaves in twos from the same sheath, with cones egg-shaped, were commonly found on the shore in a sandy and poor soil." (This is an excellent description of red pine's distinguishing botanical characters.) On the portage, "almost along the whole way, we had mostly pine woods around us" . . . [which] . . . "consisted in part of red and white pine . . . ."

That eminent Philadelphian, John Bartram (unpublished notes 1753), visited the northeastern Catskills in the autumn of 1753 with intent to collect seed. At the North Kaaterskill Lake he "could see but one cone of ye two leaved pine." Later in the account, he lists among "ye trees and shrubs of ye mountain" the "two long leaved pine." These references are certainly to *Pinus resinosa* for he also lists "white pine" and "three leaved pine" (*P. rigida*). Bartram, having visited the Catskills in 1741 and again in 1742, apparently knew about this red pine station beforehand.

Specimens collected near Keuka Lake by Folwell, in 1831–32 are now in the Cornell Herbarium. In 1845, Sartwell also listed it among the trees of the western Finger Lakes region. Vasey is authority for its presence on the "pine plains of Rome," an area of fine sand lying immediately east of Oneida Lake. These two records, together with one from Pearson, in the Helderbergs, were reported by Paine (1865). Between 1867 and 1899, Peck reported or collected it from several stations. The red pine stands along the brink of the Genesee Gorge at Portage, noted by Clinton in 1865, have since been reported by other observers. Dudley (1886) listed nine stations from the vicinity of Ithaca.

LeRoy (1872) reported red pine from Inwood, the extreme north tip of Manhattan Island, but subsequent workers have chosen to ignore the record. Inwood is a rocky knob rising steeply from the river; it has always been and still is a park. It is the site of a considerable number of unusual botanical records and its characteristics are such as would make it suitable for red pine. LeRoy was a good botanist in his own right as well as a co-worker with Dr. Torrey. It seems unlikely that he would have made an incorrect identification, or that the Torrey Botanical Club would have failed to correct such an error. Even though no specimen has yet been located, we have elected to show this disjunct occurrence on our map.

Roberts and Reynolds (1938) show seven stations in Dutchess County. In the absence of substantiating specimens,

Goodrich's (1912) report for Onondaga County is considered to be doubtful and has been omitted.

The early land surveyors in New York, whose manuscript notes and maps have been studied, recorded red pine under a variety of names: red pine, Norway pine, yellow or yallow pine, and even pitch or pich pine. The earliest discovered record was made in 1788–89 by surveyors on the Phelps and Gorham Purchase (Anon. 1789) while marking the outbounds of the present towns of Caton, Corning, and Thurston and other townships now within the towns of Bath, Rathbone, and Addison, all in Steuben County and in the Chemung River drainage. Describing the west line of Township 3, Range 3 (now in Thurston), the surveyors recorded "6th mile (going north) . . . over land descending to the west, the growth yellow and white pine, the soil very poor, hard and stony to the end of the mile and to the (northwest) corner, a large yellow pine tree . . . ." Likewise, going south on the west line of Township 4, Range 3 (now in Bath) they recorded ". . . 1st mile . . . then over land descending to the south, timbered yellow and pich pine, the soil hard and stony . . . ."

Fairchild (1794), surveying Township 2, Range 2 (now Erwins) in 1794, described the timber encountered going west on the north line: "5th mile, Timber B & W Oak, W & Norway Pine, land hilly, soil stony & poor."

The westernmost occurrence of red pine in New York was first noted by Shepard in 1798, surveying north on the west line of Township 6, Range 8 of the Holland Purchase (now in the Town of Collins, Erie County); 6th mile: "W Pine, W Oak, Chestnut, Hemk, Beech, Yallow Pine, soil red loam." In 1808, Fletcher making lot surveys in the same township, described the timber as "Pine, White Oak, Black Oak, Norway Pine."

Another isolated occurrence of red pine, originally recorded as pitch pine, was first noted by Rea (1802), while running a traverse of the lower reaches of Oak Orchard Creek, in Orleans County. This station was rediscovered in 1947 by working from Rea's old field notes.

In the Lake Champlain drainage, red pine was valuable enough to have been stolen from State land. Webster in 1811, surveying the Peru Bay and Trembleau tracts, now in the towns of Chesterfield and Willsboro, Essex County, recorded an abundance of "yellow pine." Of the latter tract, Lot 16 was described as follows: "the timber principally burnt and cut off, that which remains is small yellow and white pine." In 1819, surveying State lots in what is now the Town of Plattsburg, Clinton County, Webster described one lot: "All the south part of this lot lies upon a high burnt plain . . . the yellow pine has been all cut off as is the case with all the other lots."

One of the few records of red pine on the Saratoga Sand Plain dates from 1792 when Cockburn noted "fine yellow pine timber" amidst the pitch pine and oak northeast of Saratoga Lake.

Ecology and Present Distribution

Copious records, both in the literature and the many unpublished observations and collections made by himself and his co-workers, were kept by the late Dr. Homer D. House, New York state botanist. These he very kindly made available to us. In the hope of gathering further evidence, we circularized many of our colleagues in the forestry profession. The returns nearly doubled the number of records, greatly strengthened the data for the central southern tier of counties and the northern and western Adirondacks. Records from the Cornell Herbarium, provided by Prof. R. T. Clausen, have added several new stations. Stanley J. Smith, Senior Curator of Botany of the New York State Science Service, has been of great assistance. To all those who have assisted in this work, and especially to the District Foresters of the Conservation Department and their staffs, we tender our most sincere thanks. Without such

friendly help from many people, no three men could possibly have accumulated so many new data in so short a time.

While it is unthinkable that any such endeavor can be complete, we believe that most of the important stations for native red pine in New York are shown in Figure 2. The number of stations shown is in excess of two hundred. In Clinton, Franklin, Jefferson, Schuyler, and Steuben counties red pine is so widespread and abundant that our records indicate only the towns in which it is known to occur, and not the specific locations of individual stands. These have been plotted by a single square in the center of the town. Because of its bulk, the detailed data from which Figure 2 was prepared have been omitted. However, all our records have been deposited in the New York State Museum at Albany.

Because it made excellent lumber, red pine was cut early and heavily, as evidenced by Webster's (1819) report that "the yellow pine has been all cut off" in Clinton County. But, being longlived, free from serious pests and diseases, and quite resistant to fire (Verrall 1938), it has maintained itself very well. This persistence is best illustrated by a comparison

FIG. 2. The natural distribution of red pine in New York. See text for explanation.

of modern distribution records with the reports left by early travelers and surveyors, even as long as two centuries ago. At Northwest Bay, where Peter Kalm saw it, red pine is still present on poor, sandy soils along the shore and on the nearby mountains. John Bartram's old campground at North Lake continues to bear a forest in which red pine is conspicuous. We have also located numerous red pines in the Keuka Lake-Seneca Lake area, where Folwell and Sartwell reported it.

The station in the "Helderberg mountains three miles south of Knowersville" (now Altamont, Albany County) reported by Pearson referred, we believe, to a considerable stand which local tradition said grew on the Horseshoe Lot, now a part of John Boyd Thacher Park. Although once extensive enough to have supplied wide "yellow pine" floor boards for several nearby farmhouses, this stand is now reduced to a small group of stunted trees on the brink of the cliffs. Peck's station at Sand Lake is still valid. Wiegand and Eames (1926) confirmed, forty years later, all of Dudley's (1886) stations. As noted above, red pine was found again along the lower reaches of Oak Orchard Creek, Orleans County, where it had been noted by the surveyors 145 years earlier.

Shepard's (1798) Erie County station appears to have been lost, although the New York State Museum has a specimen collected by Johnson in 1926 from "Gowanda." Although "all cut off" in 1819, red pine is still both abundant and commercially important in Clinton County. It is apparent that, despite lumbering, cultivation and fire, red pine has clung tenaciously to sites which suit it and that it now has substantially the same pattern of distribution that it had in immediately precolonial times.

The most critical period in the life of a red pine tree is its first decade, and perhaps its first two years. Seedlings require almost bare soil on which to develop; they are excluded by heavy sod or by hardwood litter. All but the lightest of overhead shade will suppress them. On damp sites, where goldenrod (*Solidago*) is abundant, seedlings may be seriously retarded by the needle rust fungus (*Coleosporium solidaginis*). Poor drainage and alkalinity in the upper soil horizon are inimical, as extensive planting experience has amply demonstrated. But, once well established on a suitable site, red pine is most persistent, as is attested by its presence, albeit in reduced numbers, at substantially all of the stations where it was recorded, fifty to two hundred years ago.

In New York, red pine often occurs in small pure stands. Many of these appear to have originated through the seeding up of a *temporarily exposed area* (Fig. 3) by a few or perhaps only a single seed tree. There is evidence that suitable seedbed conditions may be of relatively short duration, hence the tendency of these stands to be even-aged even though a continuous supply of seed was available, or to be composed of even-aged groups. More commonly, red pine grows in mixture with white pine and dry-site hardwoods. This is especially true in the Southern Tier counties and in the eastern Adirondacks.

Single red pine trees, or small groups, are sometimes found at a considerable distance from any discoverable seed source. These may represent either relics or new invaders; cases which are attributable to each have been studied. District Forester C. E. Baker (personal communication 1949) of Norwich reports that the boys from CCC Camp S–68 "found one tree about 8 inches dbh on Chenango Area 1, about a mile north of East McDonough. How it got there is a mystery, as it is well back in a natural hardwood and white pine growth." Our map shows no other station within 40 miles. Another isolated occurrance is in the Town of Stephentown, Rensselaer County. Here, in a stand of big, old-field white pine, northern hardwoods and red spruce was a single red pine, 21 inches dbh, a hundred feet tall, and 94 years old. It is apparent that both red and white pine seeded in on land newly cleared, undoubtedly by the custom-

FIG. 3. Excellent natural reproduction following clearcutting of a red pine stand on sandy soil. On such sites, pure red pine is a climax association. Northwest of Ausable Forks, Clinton County, 1938. Photograph by E. W. Littlefield.

ary procedure of cutting and burning. The known stations nearest this tree are 9 miles to the northwest and 8 miles to the south. Unfortunately, this fine tree was blown down by the Great Wind of 1950. Barring some soil-exposing cataclysm, it is unlikely that these stations will or would have persisted beyond the life of the trees now, or recently, in being.

New invasion is certainly indicated by the occasional saplings or poles, singly or in groups, which have come up on old fields, even on unfavorable soils. This is especially true in the Southern Tier, where red pine reproduction is sometimes locally abundant on abandoned agricultural lands that have been impoverished by cropping and sheet erosion.

In New York, red pine grows over a wide altitudinal range. LeRoy's (1872) station at Inwood, the northernmost tip of Manhattan Island, is a rocky knob whose elevation runs from sea level up to 220 feet. Stations at New Hamburg, and Selkirk in the Hudson Valley and on Valcour Island in Lake Champlain are in the 100–200 foot zone, while the stations along Oak Orchard Creek are at 300 feet and those at New Scotland at 400 feet. A large number of locations are in the 500 to 1,500 foot range and at least a fair number at still higher elevations. The fine stand at North Lake is at 2,130 feet. Littlefield (1940) reports that "one of the most interesting of these stations is at Silver Lake Mountain in Clinton County. The upper slopes of this peak, between 2,000 and 2,300 feet, are covered by almost pure stands of red pine." But our highest record is "a station at 2,700 feet on Whiteface Mountain. There is a single scrubby specimen a few rods east of the

top of the T-bar lift and a considerable number of trees scattered about on the slopes below the shelter" (Littlefield 1950).

The climate of New York, except for Long Island and the lower Hudson Valley, is modified continental, the modification being in the form of an occasional northeast or southeast coastal storm that increases the precipitation without much effecting the temperature. As might be expected from the proximity of two of the Great Lakes and the presence of both extensive lowlands and considerable mountain masses, the climate is varied. Red pine is found in all of the climatic range except in the higher mountains, above 2,700 feet. Whether it be Oak Orchard Creek with a relatively mild and equable climate; or Whiteface and Silver Lake mountains—hot in summer, bitter cold in winter, windy at all times; or the Cranberry Lake area, with a climatic regime resembling that of interior Alaska, red pine thrives in them all. Table I, abstracted from Mordoff (1949), indicates some climatological statistics for four representative stations where red pine is abundant. McCarthy (1939) says that at Wanakena "an average growth of 100 cu. ft. of wood per acre per year has been obtained in red pine plantations during the first 25 years." Such growth is of essentially the same magnitude as that produced in the relatively mild climate of the middle Hudson Valley or in central New York. Climate, *per se,* appears to have little direct effect upon red pine distribution in New York.

There are three reasonably distinct areas in which red pine is found in New York (Fig. 2), each satisfying in a somewhat different way the ecological requirements of good soil drainage and aeration, soil acidity, and the absence of severe plant competition.

The Adirondacks

The species is most common and widespread on the coarse sands and gravels that occur around and, at lower elevations, within the Adirondack province. These are usually deltaic or lacustrine in origin, deposited in temporary lakes during glacial ablation. The soils are excessively well-drained, chiefly sands, loamy sands or gravelly sands in texture, belonging to the Adams, Colton, Constable, and Merrimac series. In addition, the species may occasionally occur on the coarser members of the Hermon and Gloucester series, well-drained soils on loose till. Although these soils are strong to weak podzols, where red pine is found the characteristic surface organic layer (A_0) is either lacking or thin. The frequent disparity between an inconsequential organic horizon and a deep A_2 beneath, the occasional presence of charcoal, together with observations on the vegetation of nearby undisturbed areas, clearly show the relation of red pine to fire and its sub-climax position even on these coarse soils (Fig. 4). It may, however, have a more nearly climax position on coarse-textured materials bordering lakes because of the full exposure of such sites. The fine stands at Long Lake and Brantingham Lake

TABLE I. *Weather data for four representative stations within the New York range of red pine (from Mordoff 1949)*

Station	Elevation (feet)	Temperature			Growing season (days)	Mean annual precip. (inches)	Mean annual snowfall (inches)
		Min. (°F.)	Max. (°F.)	Mean temp. growing season			
Albany	277	−24	104	67	174	37	49
Elmira	863	−24	104	66	157	33	41
Plattsburg	183	−25	99	63	179	30	56
Wanakena	1510	−45	100	60	114	41	136

FIG. 4. A group of red pines at Pine Grove, Lewis County. The biggest trees range up to 18 inches at breast high and to 90 feet in height. The stand probably originated following a small fire about one hundred years ago. The advance reproduction is white pine. Photograph by Cook, 1952.

exemplify this. At its higher stations throughout the Adirondacks, red pine occurs on steep slopes and ridges where the mantle of till and detritus from the igneous bedrock is too thin and too dry to support a full plant cover.

Quite unlike other Adirondack sites is Valcour Island in Lake Champlain, five miles below Plattsburg. This is a block of Chazy limestone, often deeply fissured and often covered with only a shallow soil. Here, red pine grows in association with such calciphiles as white cedar (*Thuja occidentalis*) and ramshead ladyslipper (*Cypripedium arietinum*). The spruce on Valcour is white (*Picea glauca*), the much more common red spruce (*P. rubens*) being absent. Despite the presence of limestone as a substrate, the soils are for the most part both acid and dry.

The Central Southern Tier

The flat-bedded, gray, acid Devonian sandstones, siltstones, and shales of the Allegany Plateau exhibit only moderate differences in hardness. Slopes shaped by ice action tend, even when steep, to be smooth in outline and uniformly veneered with till. With but occasional exceptions, such slopes originally supported a mesic forest from which red pine was absent.

The numerous occurrences of red pine in this region lie within the Susquehanna River drainage and the deep valleys opening through to the north. This was an area of violent glacial action, where the south-moving ice deepened the valleys now occupied by the Finger Lakes, plowed out their southern headwaters and oversteepened the gaps along the divides.

Farther south, there are deep valleys cut by melt-water (Von Engeln 1945). Thus, geomorphically, this section is marked by numerous narrow valleys with steep walls, deeply incised into the ancient peneplane. The walls of these valleys, and those of the Finger Lakes as well, have, in turn, been cut by the post-glacial gorges of their lesser tributaries.

An interesting circumstance develops here. The bedrock dips gently to the south. Despite their aspect, the north-facing slopes are often as dry, because of drainage down the strata, as the south-facing slopes across the valley, a complete reversal of the usual situation. Thus, to a greater degree than in the rest of the Southern Tier, this section provides a relative abundance of xeric, precipitous, rocky slopes. Although occupying only a small gross area, they are, in terms of seeding range, either juxtaposed or intermittently connected. Exposed, acid, and dry, these declivities afford refuge for species with characteristics like red pine, and are presumed to be responsible for its survival there.

The soils of the slopes and slope margins on which red pine occurs are shallow and quasi-residual, consisting of local

materials transported by ice and creep, together with those weathered in place. Excessively drained by reason of slope and shallowness, acid and friable throughout, they are mapped as steep phases of Lordstown stony or flaggy silt loam or as rough, stony land of Lordstown materials.

Following disturbance, red pine may spread to adjacent, less precipitous Lordstown areas and to well-drained, gravelly soils such as the Chenango and Otisville series.

The Capital District

The third area of concentration is less homogeneous than the other two and can be separated from them only imperfectly. To the west of the Hudson Valley, it includes the northeastern corner of the Allegany Plateau. Unlike the Plateau in the Central Southern Tier, the strata here are quite varied and include such resistant beds as the Coeymans and Onondaga limestones and the Reidsville flags. These impart to the topography a step-like pattern of terraces alternated with steep to precipitous slopes; it is along these terrace margins that red pine is found, on soils of Lordstown material or affinity. In the northern Catskills, lying to the south of and stratigraphically higher than the Allegany Plateau, red pine is found on steep slopes and dry benches.

East of the Hudson Valley, three stations are known on the Rensselaer Grit Plateau: on a rocky slope along its west flank, on the slope above and on the margin of the gorge of the Poestenkill, and on unnamed rocky soil in the upper drainage of Black River. Farther south, it is found on dry shale ridges in Columbia and Dutchess counties.

In the lowlands, red pine occurs on deltaic glacial gravels of such tributaries as the Hoosic and the Kinderhook, and on the gravelly north ends of drumlins in the area around New Scotland.

Two stations, considerably disjunct, occur in western New York. Northwest of Gowanda, Erie County, and adjoining the Cattaraugus Indian Reservation, is the station reported by Shepard in 1798. This lies upon a broad hilltop between Cattaraugus Creek on the south and Clear Creek, an area whose characteristics closely resemble those of red pine sites in the Chemung drainage, further to the east. Johnson collected here in 1926, but a reconnaissance in 1949 failed to find any surviving trees. Perhaps the stand has been eliminated by recent land clearing. However, we feel that an intensive botanical exploration should be made before the station is marked as lost.

Along Oak Orchard Creek, within a mile of its mouth red pines occur in small groups, confined by cultivation to the steep banks of the stream, here cut into Queenston shale. The acid, well-drained nature of this site is indicated not only by its physical character but also by the presence of sassafras (*Sassafras albidum*), blueberry (*Vaccinium* sp.), and Jerseytea (*Ceanothus americanus*). The "oak orchard" at the mouth of the creek was a favorite eighteenth century camping place for Indians, fur traders, and both French and British military forces. It was the terminus of an important path coming up from the Iroquois towns to the south. Woodland fires may have helped to preserve this little outlier of red pine.

Perhaps it is equally important to know where red pine does not and apparently did not occur naturally. From the foregoing discussion, one might anticipate its absence from those areas where soil and topography favored unbroken stretches of mesic forest, even apart from any specific effects of soil drainage or alkalinity. Red pine is, in fact, absent from the lacustrine and till plains south of Lake Ontario and in the Mohawk and Hudson Valleys. These are marked by level to undulating topography and a deep mantle of medium to fine textured soil, often influenced by lime. Interesting exceptions are the outliers along Cattaraugus Creek and Oak Orchard Creek.

Red pine is also absent from the ice-smoothed northward margin of the Allegany Plateau and from the gently rolling,

poorly drained hilltops of the entire Plateau region. It has not been recorded in any of the plant lists from the thoroughly-studied Allegany State Park, an unglaciated area within the great bend of the Allegany River. Moreover, in New York it is apparently lacking from the entire Allegany River watershed and from that of the Genesee south of its postglacial gorge at Letchworth Park. However, this may be due to soil factors alone, since Ibberson (1949) indicates its presence on both watersheds just across the line in Pennsylvania. On the other hand, it may be due simply to inadequate botanical collecting.

The eastern Susquehanna and the Delaware watersheds are ancient, mature, south-flowing drainage systems. Red pine has been reported only sporadically within this area. Here, too, more intensive collecting is needed.

However, a topographic explanation cannot account for the absence of red pine from rocky slopes in the southern Catskills, the Shawangunks, and the Hudson Highlands on both sides of the river, where ridges are often occupied by forests of chestnut oak (*Quercus prinus*) or by a fire disclimax of blueberries and stunted pitch pine. That red pine is not wholly absent, however, is attested by a group of forty trees on the top of Breakneck Mountain, the northernmost pinnacle of Wawayanda Mountain and only two miles south of the state line, in New Jersey. This is considerably disjunct from the range both in southern New York and in eastern Pennsylvania.

To the best of our knowledge, the species is not to be found on Tug Hill. This plateau rises sharply from the Lake Ontario lowlands and receives heavy orographic precipitation. Although some areas of soil (Constable) suitable for red pine occur, this is mostly a land of immature drainage and heavy soils, sodden in spring and fall. It is isolated from the main red pine range, which lies to the east, on the other side of the Black River Valley. Hotchkiss (1932) fails to list it and no stations are known to us or to the foresters of the district.

Although soil and moisture conditions appear to be favorable and planted trees do well on them, red pine is almost completely absent from the Saratoga Sand Plain and the Rome Plains. The former is a belt of aeolian, sandy soil, mostly Colonie fine sandy loam and related soils, lying along the west side of the Hudson River, from Albany to and beyond Glens Falls. The original forest was of large white pine and oak, although survey records by Cockburn (1769) show that parts of the Sand Plain were even then covered mostly by pitch pine. The present gray birch (*Betula populifolia*)–pitch pine–scrub oak (*Quercus ilicifolia*)–little bluestem (*Andropogon*) association is a fire disclimax, induced by almost annual spring burning. Three stations are of record, one already engulfed by suburban development. Two are in the extreme southwest corner, the third east of Saratoga Lake. The Rome Plains, an essentially similar area, has likewise been reduced to a gray birch–bluestem barren. The late Dr. House, a native of Oneida County, was never able to confirm Vasey's old record. The red and white pine forest south of the head of Lake George, that Kalm saw in 1749, is gone, the association now being white pine–pitch pine–gray birch. The failure of red pine to reestablish itself on these areas following agricultural abandonment may be associated with a very low fertility status brought about by excessive cropping of these coarse-textured soils. Conifers planted thereon often exhibit severe nutrient deficiency symptoms (Heiberg and White 1950).

East of the upper Hudson River, the absence of the species from all but northwestern Washington County, an area of granite hills and gravels, coincides with an area of lacustrine clays and till from calcareous sandstone.

Long Island is characterized by terminal morains and outwash plains. When first visited by white men, it had a considerable

Indian population, among whom the burning of the pitch pine forest was an annual custom. The present flora is largely a fire type of stunted pitch pine and depauperate oaks.

The scattered occurrence of red pine outside the Adirondacks suggests a relic position, the remnants of a distribution formerly more abundant and widespread. Lacking positive evidence, as from pollen analyses, the hypothesis is scarcely debatable but some qualifications of it are apparent. Even during the period of pine maximum which followed the complete ablation of the Wisconsin ice, red pine would have been at a decided disadvantage in competition with white pine and other mesic species on the heavier soils, although perhaps less confined than now. If its former range had extended into the areas from which it is now absent, one might expect to find numerous small disjuncts in the occasional isolated spots of favorable habitat adjacent to its present range, as in the western Allegany Plateau and Catskill areas. This is not the case.

Red pine still occupies not only the same general areas but sometimes even the same ten-acre patches that it did when recorded by the early botanists, travelers, and land surveyors during the period from 1749 to 1865. It has been extirpated from surprisingly few stations and from these only by violent ecological changes resulting in fundamental impoverishment of the soil. Even such seemingly vulnerable populations as those along Oak Orchard Creek, or on Breakneck Mountain or Valcour Island have clung successfully to their tenuous roothold. Conversely, there are few places where red pine seems to be extending its range and these appear to be transitory eruptions into sites affording temporarily suitable seedbed conditions, but where the species can scarcely be expected to reproduce itself.

Summary

Red pine is the finest of the hard pine group in the Northeast. It is a component of the Hemlock-White Pine-Northern Hardwood forest, with which its range is practically coextensive. This range extends from the upper Great Lakes to the Atlantic Coast and to Newfoundland, with two disjuncts in West Virginia. In New York, the species is widely but irregularly distributed, being restricted to areas of excessively-drained, acid soil. There are three principal centers of distribution: the Adirondacks, the central Southern Tier, and the Capital District. Outliers are found along Oak Orchard Creek in Orleans County, near Gowanda in Erie County, and in the north tip of Manhattan Island. A fourth is on Breakneck Mountain, just over the line in northern New Jersey. This tree is absent from the great till plain south of Lake Ontario, from the central and western segments of the Allegany Plateau, from the southeastern corner of the State and from Long Island.

Outside the Adirondacks, the distribution pattern is such as might indicate that red pine is a relic species, a holdover from some post-glacial period when the climate was both warmer and drier than now. However, the absence of outliers on small patches of suitable site in the extensive areas where the species does not now occur argues against this. Even under a drier climate, red pine would be at a considerable competitive disadvantage to white pine and other mesic species on the heavier soils.

To those areas which meet its ecological requirements, and where it was reported by travelers and surveyors a century or two ago, red pine has clung tenaciously and neither lumbering nor fire has driven it from its ancient domain.

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MEAN DEPTH AND THE FISH PRODUCTION OF LARGE LAKES

D. S. Rawson

Department of Biology University of Saskatchewan, Saskatoon, Saskatchewan

Introduction

The understanding, measurement and prediction of biological productivity may be regarded as the central problem of limnology. Investigators have been impressed and sometimes discouraged by the complexity of the situation and the problems of satisfactory measurement. It is difficult to measure even the standing crops of organisms and very difficult to discover their rates of production and utilization. Nevertheless it is important that we should make frequent and bold attacks on the problem to consolidate our findings, and thus to give intelligent direction to further investigations. The author has maintained (Rawson 1939, 1942) that the factors affecting lake productivity may be considered conveniently in three groups, morphometric, edaphic and climatic. The present contribution is an attempt to show that in the Great Lakes and in several large lakes of western Canada, morphometric factors are dominant.

The Morphometric Factor and Measures of Productivity

The shape of the basin has long been recognized as an important factor in limiting the production of plants and animals in a lake. Thienemann (1927) was the first to develop this concept which was later combined with Naumann's (1929) classification of obligotrophy and eutrophy which had been based on regional water types and their effects on plankton development. Lundbeck (1934) clarified the situation by distinguishing primary or edaphic oligotrophy, due to the chemical nature of the water, from secondary or morphometric oligotrophy which was the result of the shape of the basin.

The depth of a lake has direct effects on its temperature, stratification, circulation and on the dilution of nutrient materials. Depth also has indirect effects on the circulation or loss of nutrients and on the distribution and numbers of organisms. Thienemann was therefore quite justified in emphasizing mean depth as a most significant factor in determining lake type. Since oligotrophy and eutrophy intergrade we can have no absolute division. Nevertheless Thienemann's arbitrary division at a mean depth of 18 metres, where the volume of the epilimnion is approximately equal to that of the hypolimnion, appears to be satisfactory in most lakes when judged by biological indices.

The accurate measurement of lake productivity is still a hope for the future. The standing crops of plankton and benthic organisms are difficult to measure and it seems probable that standing crops often bear no close or constant relation to real production. The ingenious use of hypolimnial oxygen deficits by Strøm (1931) and Hutchinson (1938) appears to give us some measure of the "basal metabolism" of a lake. Recent work by Lindeman (1942), Clarke (1946) and Riley (1940; Riley *et al.* 1949) has combined practical observations with a theoretical attack on the problems of energy levels and the transformation of nutritive materials from the primary photosynthetic production up the scale toward fish production. While this approach is being developed it seems possible that we may make some progress by considering the final stage of lake production, the fish. Because of physical and economic limitations on fishing, the annual catch of fish in a lake may rarely approach its maximum productive capacity. However the long-term average catch in lakes which are extensively fished gives

us useful evidence concerning the possible production.

TABLE I. *Commercial fish production from Lakes Winnipeg, Winnipegosis and Manitoba, 1900 to 1950*

Year	Lake Winnipeg	Lake Winnipegosis	Lake Manitoba
1900		2,852,900	883,000
1901		5,671,900	2,781,200
1902		5,857,200	3,550,000
1903		6,062,000	4,350,000
1904		5,578,000	4,866,000
1905		4,831,000	3,691,000
1906		3,163,000	2,714,000
1907/08		2,461,000	1,972,000
1908/09		2,149,200	1,931,500
1909/10		3,547,100	4,144,900
1910/11		4,444,800	8,345,700
1911/12		3,898,400	3,218,600
1912/13		4,245,000	3,093,600
1913/14		4,750,600	1,027,500
1914/15		4,599,100	4,068,800
1915/16		2,974,700	2,515,600
1916/17		5,452,600	3,941,500
1917/18		5,543,900	3,941,500
1918/19		no record	no record
1919/20		5,279,600	3,085,000
1920/21		4,866,000	1,811,500
1921/22	8,044,000	3,547,300	1,983,600
1922/23	8,201,900	4,534,600	2,565,500
1923/24	6,647,400	5,109,400	4,855,800
1924/25	8,408,300	4,129,900	5,158,700
1925/26	11,050,300	5,523,300	8,525,600
1926/27	15,386,100	6,460,400	7,785,800
1927/28	15,936,400	5,715,500	5,746,300
1928/29	16,006,800	7,005,300	5,662,500
1929/30	15,343,100	5,175,000	3,658,400
1930/31	11,526,800	3,950,700	3,210,600
1931/32	8,341,800	2,931,600	4,496,800
1932/33	10,294,600	2,293,200	4,870,300
1933/34	12,624,500	3,150,800	5,035,000
1934/35	13,164,100	3,010,300	4,281,600
1935/36	11,067,300	4,978,100	6,888,800
1936/37	14,352,200	6,098,000	6,106,100
1937/38	14,912,300	6,405,000	5,855,200
1938/39	18,533,600	6,419,500	7,283,300
1939/40	15,633,300	5,306,300	5,627,000
1940/41	21,895,200	5,430,500	9,386,500
1941/42	20,162,100	5,557,100	8,975,500
1942/43	17,690,300	7,539,000	5,774,000
1943/44	18,177,100	7,129,800	3,720,100
1944/45	13,753,500	6,062,200	4,077,700
1945/46	16,330,300	5,700,900	5,952,800
1946/47	14,309,200	4,637,100	4,112,000
1947/48	16,438,100	4,873,800	3,400,700
1948/49	16,447,500	4,632,500	3,948,700
1949/50	17,310,800	3,862,500	3,563,800

LONG-TERM RECORDS OF FISH PRODUCTION

The annual commercial catches in small lakes tend to show wide and erratic variations from year to year and through periods of years. It is relatively easy to overfish a small lake to the stage where it must be closed to allow for recovery. Also the small fishery is more vulnerable to economic changes and may be dropped in periods of poor markets. In large lakes the fish population is less readily disturbed. Also the large investment in the fishing operation provides a strong incentive to continue production. If the catch of one species diminishes the fishermen will attempt to harvest another. Thus the total fish production from large lakes may be expected to reflect something of their productive capacity.

Records for the large lakes in Manitoba have been obtained from the Department of Mines and Natural Resources, Winnipeg. These are of considerable interest and, since they have not been published elsewhere, they are reproduced here as Table I. It will be noted that Lake Winnipeg has been producing during the past 25 years at a rate in excess of 15 million pounds per year and that Winnipegosis and Manitoba each average more than 5 million pounds per year. In Lake Winnipegosis the average for the 25-year period 1926 to 1950 is greater than that for the preceding 25 years by 18 percent. Production from Lake Manitoba in the period 1926 to 1950 has averaged 30 percent more than that of the previous 25 years. Records for Lake Winnipeg go back only to 1921 but the average production in the second fifteen years of this period exceeded that of the first by 53 percent.

The catch statistics for the Great Lakes over an extensive period are available in the report of the International Board of Inquiry (1943). It is of interest to compare the average production in two consecutive 25-year periods 1891–1915 and 1916 to 1940. This has been done and Table II shows the result, expressed in

TABLE II. *Comparison of the commercial fish production in eight large lakes in two successive 25-year periods*

Lake	Average annual fish production				Percentage change
	First 25 years		Second 25 years		
	Total pounds	Pounds per acre	Total pounds	Pounds per acre	
Superior	18,470,600	0.91	16,945,200	0.83	− 8.8
Huron	26,520,800	1.80	20,211,000	1.38	−23.3
Michigan	35,435,800	2.47	22,856,000	1.59	−35.6
Erie	55,216,200	8.68	46,480,400	7.30	−15.9
Ontario	4,245,400	0.88	4,780,400	0.99	+12.6
Winnipeg	10,731,700	1.84	16,400,800	2.82	+53.2
Winnipegosis	4,389,300	3.28	5,193,900	3.88	+18.3
Manitoba	3,354,000	2.88	5,517,700	4.75	+30.1

Note: For the Great Lakes the 25-year periods are 1891–1915 and 1916–1940. For the Manitoba lakes the periods are 1901–1925 and 1926–1950, except for Lake Winnipeg in which two 15-year periods, 1921–1935 and 1936–1950, are compared.

pounds per acre. In four lakes the production in the second period was smaller by amounts between 9 and 42.5 percent. In Lake Ontario the average catch in the second period increased by 12.5 percent.

The observation that the average production of each of the Great Lakes (except Ontario) decreased in the second of two 25-year periods while it increased in each of the large Manitoba lakes suggests that the Great Lakes have been fished close to or somewhat beyond their long-term productive capacity while the Manitoba lakes may still be capable of increased average production. This is a matter of special interest in relation to our later analysis.

MEAN DEPTH AND FISH PRODUCTION

The long-term average production was calculated for a number of large lakes and reduced for comparative purposes to a basis of pounds per acre. Table III includes these data for the six Great Lakes, Lake Nipigon, and five large lakes of western Canada. It was not possible to use the same 25-year period for all of the lakes. In the Great Lakes the period 1916 to 1940 was used except for Lake St. Clair where records for this period are incomplete and data for 1891–1915 were substituted. The Lake Nipigon data are for the period 1918–1943, Lake of the Woods 1916 to 1940 and for the three large Manitoba lakes 1926–1950. The differences in production per unit area are rather striking, with a range from 0.83 pounds per acre in Lake Superior to 7.3 in Erie. Undoubtedly degrees of utilization enter into these values. The scattered fish population of deep lakes is obviously more difficult to harvest than the more concentrated population of shallow lakes. However, it seems probable that the data reflect also real differences in productive capacity.

TABLE III. *Mean depth, area and 25-year average fish production in twelve large lakes*

Lake	Mean depth feet	Area square miles	25-year average fish production	
			1000's of pounds	pounds per acre
St. Clair	10	460	1.680	5.72
Manitoba	16	1,817	5.518	4.75
Winnipegosis	20	2,086	5.194	3.88
Lesser Slave	22	461	1.976	6.69
Lake of the Woods	26	1,378	4.049	4.60
Winnipeg	43	8,829	15.067	2.66
Erie	58	9,940	46.480	7.30
Nipigon	180	1,875	1.280	1.07
Huron	195	23,010	20.211	1.38
Great Slave	204	10,500	9.000*	1.34
Ontario	264	7,540	4.780	0.99
Michigan	276	22,400	22.856	1.59
Superior	487	31,820	16.945	0.83

* Present annual limit (1951). Fished only 5 years.

The reasons for differences in basic productivity are presumably edaphic, morphometric or climatic.

Some consideration has been given to the edaphic situation in the Great Lakes using the total mineral content as a crude indicator (Rawson 1951a). Superior, the uppermost of the Great Lakes, has the lowest mineral content and the lowest fish production. However, Lake Ontario has a slightly higher mineral content than Lake Erie but it has produced only one-ninth as much fish per unit area. It is possible that Lake Erie may be receiving from its local drainage certain nutritive materials in much larger quantities than those available in Lake Ontario. This is not believed to be the main explanation for the wide difference in fish production.

Adequate data for a comparison of the climatic conditions in the lakes in question are not yet available. It would be desirable to compare the mean temperatures at midsummer of the upper ten-metre stratum since this includes the main trophogenic region. Lacking this information we may compare the mean monthly surface temperatures compiled by the United States Lake Survey for the years 1904 to 1943. Combining the means for July and August the surface temperatures are as follows: Superior 49, Michigan 64, Huron 65, Ontario 66 and Erie 72° F. The very high surface temperature of Lake Erie is of special interest in relation to its high fish production.

The morphometric differences seemed to relate to the observed variation in fish production more closely than did the edaphic or climatic conditions. Therefore the mean depth, as the chief index to morphology, was included in Table III and plotted against average fish production in Figure 1. The shallow lakes, with mean depths in the eutrophic range (less than 60 feet), have fish productions between 2.5 and 7.5 pounds per acre. The deep oligotrophic lakes have productions

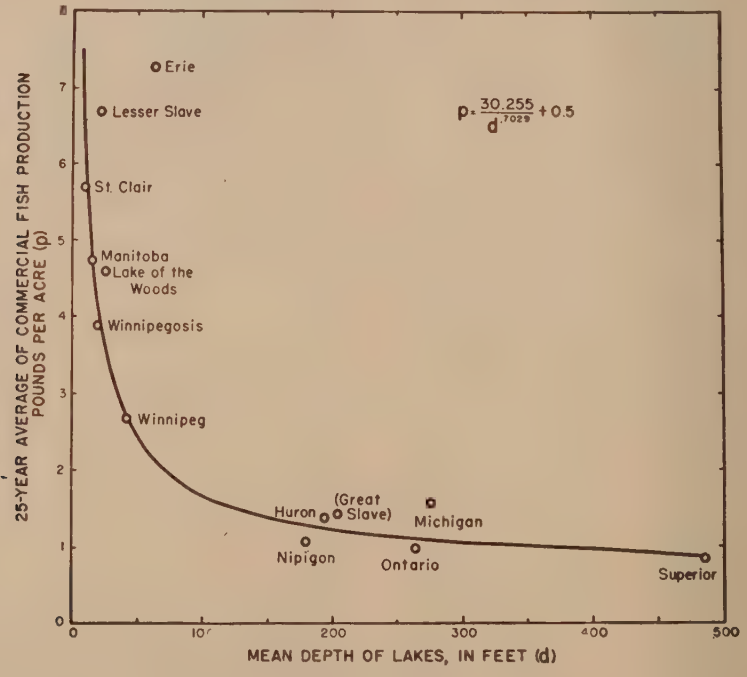

FIG. 1. The relation between mean depth and long-term fish production in 13 large lakes.

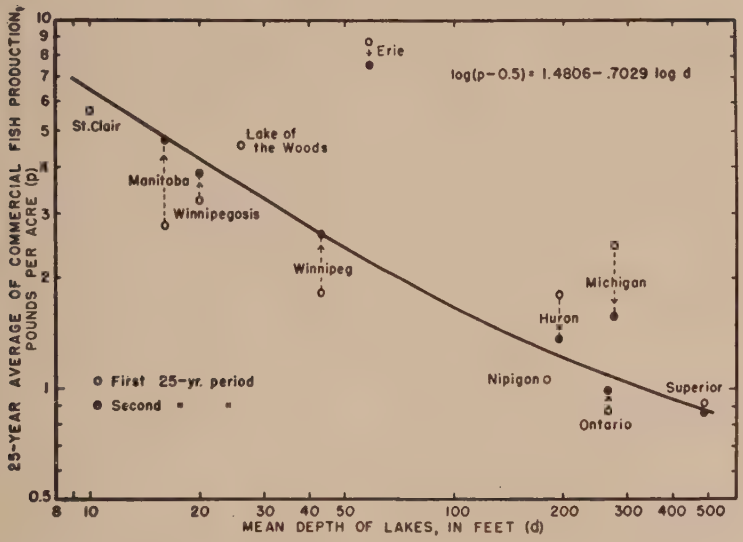

FIG. 2. Logarithmic plot of the relation between mean depth and average fish production for one or two 25-year periods in 11 large lakes.

between 0.8 and 1.6 pounds per acre. The curve drawn through points in Figure 1 suggested a logarithmic relationship so the data have been plotted on logarithmic coordinates in Figure 2. In the second graph also there are plotted the average rates of production for the earlier period of 25 years as shown in Table II. It is noteworthy that in every case where data are available for two 25-year periods, the rate of production in the second period comes closer to the curve than that for the first. This suggests that the growth of fishing in the three Manitoba lakes has brought them toward their reasonable productive capacity. On the other hand Lakes Erie, Huron and Michigan show considerable decreases in their second 25-year period suggesting that they may have been overfished and that production is being adjusted toward a lower sustainable yield. No doubt part of the drop in Lake Erie can be attributed to the change from an early fishery relying heavily on plankton feeders to a later production depending mostly on the less efficient piscivores. Such explanations are, of course, highly speculative.

The general interpretation of the data presented is that morphometric factors, represented here by mean depth, are predominant in determining the fish production of most of these lakes. That some lakes should be divergent is not surprising when we recall that our data represent utilization rather than productive capacity and that other factors, edaphic or climatic in nature, are known to affect productivity. Thus the degree of divergence of any lake from the supposed relation is worthy of special consideration.

Lake Erie is the most divergent of the lakes in question. Its production is more than three times that suggested by the curve for a lake of 58 feet mean depth. Several suggestions can be made as to reasons for this situation. Perhaps the very large and highly productive shallow area of western Lake Erie so outweighs the deep, less productive eastern end that the average production is not characteristic of a lake of 58 feet mean depth. In other words the form of its bathymetric curve may provide a clue to its divergence from the general relation. It is believed that fuller utilization is partly responsible.

In Lake Erie a wide variety of species are heavily fished. In Lake Ontario, by contrast, a very abundant species, the alewife, is hardly touched by the commercial fishing. Lake Erie has been noted above as the most southern of the lakes under consideration. Being also shallow, its summer temperatures are considerably warmer than any of the other Great Lakes. Perhaps also the rich agricultural drainage and heavy fertilization by sewage provides a greater supply of nutrients than is found in the other lakes. Thus Lake Erie could be more productive than the others because of entirely favourable morphometry, climate and edaphic conditions. Lake Superior, at the other extreme, appears to have entirely unfavourable morphometry, climate and edaphic conditions, or in other words, it is harmonic for the conditions of extreme oligotrophy.

Lesser Slave Lake also shows a production rate well above the average for lakes of its depth. Moreover, Dr. R. B. Miller, who provided the data for this lake, calls attention to the fact that its heavy cisco population has not been fully utilized. Thus it could have been even more divergent. It has been included as a warning that individual lakes may far exceed the rates of production suggested by the curves in Figures 1 and 2.

Lake Nipigon is the most divergent of the lakes below the line. This may well be simply underfishing. It should be noted however that Lake Nipigon is the only one of the series which lies entirely on the Precambrian shield and may thus be presumed to be in the least favourable edaphic situation.

Lake Michigan has had the highest production per unit area of the four deep oligotrophic members of the Great Lakes chain. Table II indicates that the production from Lake Michigan suffered the largest decrease, 35.6 percent, during the fifty-year period. Perhaps it has been overfished.

Great Slave Lake has been fished for only five years but it is plotted on the graph (Fig. 1) to illustrate a possible application of the depth-production curve. The present annual limit on production for Great Slave Lake is 9 million pounds and this brings it fairly close to the curve. It should be noted that the controlled fishery on Great Slave Lake was initiated at a much lower level (Rawson 1949). The limit has been advanced to the present level by stages and only after intensive sampling failed to reveal any unfavourable changes in the fish population.

Mathematical Analysis of the Data

A mathematical analysis of the correlation between mean depth and fish production was undertaken with some misgivings. The error in the calculations of mean depth probably ranges from 2 to 5 percent. The statistics of fish production may be of the same basic accuracy but considerable errors are introduced by lumping together figures for dressed and round fish. These considerations make minute mathematical calculations misleading. Also, it would be unfortunate if the equation for curves in Figures 1 and 2 should be interpreted as implying a law of productivity. The curve presents, in a simple way, a generalization concerning the average fish production in certain large lakes of various depths. That their potential productivity may be much higher is suggested by common sense and by the divergence of points representing Lake Erie and Lesser Slave Lake. Nevertheless the form of the curve is of some interest apart from the considerations of the reliability of the data.

A statistical analysis of the values in Table III indicates that a reasonably good fit can be obtained with a curve of the equation

$$p = \frac{30.255}{d^{0.7029}} + 0.5,$$

p being the long-term average fish production in pounds per acre and d the mean depth in feet. The constant, 0.5, was determined by inspection. It implies that a lake of infinite depth would still produce a small crop of fish. This is the equa-

TABLE IV. *Comparison of actual fish production from twelve lakes with expected values calculated from the observed relation between mean depth and long-term production*

Lake	Mean depth, feet	25-year average fish production, pounds per acre	Calculated theoretical production, pounds per acre
St. Clair	10	5.72	6.49
Manitoba	16	4.75	4.81
Winnipegosis	20	3.88	4.18
Lesser Slave	22	6.69	3.95
Lake of the Woods	26	4.60	3.56
Winnipeg	43	2.66	2.65
Erie	58	7.30	2.25
Nipigon	180	1.07	1.29
Huron	195	1.38	1.24
Ontario	264	0.99	1.10
Michigan	276	1.59	1.08
Superior	487	0.83	0.89

tion for the curve which appears in Figures 1 and 2. The logarithmic form, $\log (p - 0.5) = 1.4806 - .7029(\log d)$, may be more convenient. An analysis of the relationship in ten lakes (excluding Erie, Lesser and Great Slave for reasons suggested above) gives the very high index of correlation of 0.96. However, if the value for Lake Erie is included the index falls to the scarcely significant value 0.53. This is a further reminder that we should regard the curve as a guide to the average production of certain lakes and not as a universal rule. It is obvious that a multiple correlation analysis should be made when more data relating to climatic and edaphic factors are available.

Using the formula

$$p = \frac{30.255}{d^{0.7029}} + 0.5,$$

the "expected" productions of the lakes under consideration may be calculated for comparison with the actual average productions. This has been done in Table IV. Again, it will be seen that agreement is good for ten of the lakes but the calculated values for Lake Erie and Lesser Slave are very much less than their sustained production. As indicated above the constant 0.5 in the equation implies that even in a very deep lake the production would not drop below 0.5 pounds per acre. This might be interpreted as representing a limnetic productivity, that is the production through plankton and plankton-feeders in areas where the bottom fauna and bottom feeding fish are absent or present in only insignificant quantities. This might be regarded as highly hypothetical but investigations of the open water in Great Bear Lake by Miller (1947) and of McLeod Bay at Great Slave Lake by Rawson (1951b) show that conditions essentially similar to this may exist.

The curve in Figure 1 may be described as having two arms; one through points representing deep oligotrophic lakes and the other through shallow mesotrophic or truly eutrophic types. The dividing point comes close to the mean depth of 18 metres (59 feet) which is the theoretical morphometric division between oligotrophic and eutrophic types. The writer has obtained similar curves by plotting standing crops of plankton (Rawson 1952) and bottom fauna against mean depth. The close resemblance between the curve for fish production and those for basic food organisms strengthens our conviction that the relation is worthy of further study.

Application of the Relation between Depth and Production

It is possible that some use may be made of the observed relation to predict the extent of a new fishery. It was noted above that the present limit on Great Slave Lake comes close to the curve in Figure 1. Since most large, potential fishing lakes are already exploited, opportunities for prediction may be infrequent. It is important however to have rough norms for the evaluation of the production in lakes already fished. Rounsefell (1946) assembled most of the available data as to fish production in freshwater areas and has analysed it with respect to area. In 100 lakes, mostly of small size, he found a rapid decline in production per unit area as the lakes increase in size. Regressions for game and commercial fish yields were derived and calculated probable produc-

tions were presented in a useful table. Rounsefell's analysis is quite complete for small lakes and reservoirs but less satisfactory for large lakes. He includes eight of the 12 lakes listed in Table III but the production figures quoted are for the yield of a single year.

The question arises as to whether fish production is more closely related to area or to depth. Since large lakes are usually deeper than small lakes it is difficult to tell which factor is more active. However, if the production per unit area for the lakes listed in Table III is plotted against their areas, the correlation is much poorer than that of production with depth as shown in Figures 1 and 2. The writer has suggested (Rawson 1930) that increase in both depth and area is accompanied by a decrease in the amount of bottom fauna in a lake. Presumably this may be true also of fish production. The present data for long-term production in large lakes suggest that greater depth continues to effect a decrease in fish production well beyond the limit where increase in area has any important effect.

In conclusion it may be said that information on mean depth and long-term fish production in 12 large lakes suggests that the morphometric influence is dominant in determining their fish production. Deviations from the calculated relationship are observed and should be expected since edaphic and climatic factors also influence productivity.

Acknowledgments

The writer expresses his sincere thanks to the several individuals and organizations who kindly provided information used in this analysis. The United States Lake Survey provided mean depths for the Great Lakes. Mr. H. H. MacKay of the Ontario Department of Lands and Forests supplied depth and production data for Lake Nipigon. Mr. G. W. Malaher of the Manitoba Department of Mines and Natural Resources furnished data on Manitoba lakes. Dr. W. A. Kennedy provided information on depth and area of Lake Winnipeg. Dr. K. D. Carlander of Iowa State College furnished depth and fish production data for Lake of the Woods, and Dr. R. B. Miller of the University of Alberta provided depth and production figures for Lesser Slave Lake.

Summary

The factors affecting the productivity of lakes may be considered in three groups, morphometric, edaphic and climatic. It is believed that long-term commercial fish production in large lakes bears some relation to their basic productivity and that mean depth is the best indicator of morphometric conditions. Analysis of the available information for 12 large lakes demonstrates a close correlation between mean depth and long-term fish production. It is therefore suggested that morphometric factors are dominant in determining the fish production in the Great Lakes and in a number of other large lakes of central and western Canada.

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EFFECT OF COPPER SULFATE WEED TREATMENT ON BACTERIA IN LAKE BOTTOMS [1]

GERALD H. WATSON [2] AND WALTER B. BOLLEN [3]

Oregon Agricultural Experiment Station, Corvallis, Oregon

INTRODUCTION

Copper sulfate was applied to several areas of certain Oregon coastal lakes in 1947 and 1948 to control increasingly heavy growth of Brazilian water weed, *Anacharis densa* (Planchon) Victorin. Concentration of the compound effective against the weed exceeded the safe limit for fish and fish food organisms, and its general use was considered undesirable in view of the fish and game values of the lakes. Nevertheless, to alleviate the clogging of certain channels required for boating and for the towing of logs, herbicidal concentrations of copper sulfate were applied in these areas. Since it is believed that bacteria play an important role in the chain of lake productivity the question arose as to whether or not these organisms on the lake bottom were affected by the copper sulfate treatments.

Previous investigations have established certain characteristics of marine and lake bottoms and of their autochthonous microflora. Relatively few bacteria are found in coarse marine sand in shallow water; higher numbers are found in finer sediments and are attributed primarily to the higher organic content. Numbers of bacteria in lake bottoms have been found to increase as humus-like material becomes more abundant. Decay of algal crops killed by copper sulfate is often accompanied by a great increase in bacteria, but the concentration of copper employed to control algae is usually less than 0.1 p.p.m.

Waksman *et al.* (1943) observed that up to 40 p.p.m. $CuSO_4 \cdot 5H_2O$ in a plating medium had no appreciable influence on numbers of bacteria determined in sea water. Larger concentrations, up to the equivalent of 51 p.p.m. Cu, when added directly to the sea water, first depressed and then stimulated the bacteria. Some of these had a definite affinity for copper and could tolerate up to 500 p.p.m. of copper sulfate. These "copper bacteria" formed colonies with characteristic red-brown pigment which later disappeared in zones. While such bacteria developed readily in sea water to which 100 p.p.m. $CuSO_4 \cdot 5H_2O$ was added, they could not be obtained from pond water or soil. According to Manns and Russell (1934) copper sulfate markedly stimulated the *Bacillus fluorescens* group in a Maryland soil.

The biological role of copper is varied and the concentrations involved in inhibitions, deficiencies, and stimulations cover a great range according to the organisms and conditions concerned. Copper is an essential minor element. For microorganisms, concentrations of from 0.2 to 2 p.p.m. are generally added to synthetic culture media. Even slight increases over such values may prove toxic, and the toxic effects in many cases are unusually specific. Copper sulfate used for control of algae generally does not affect aquatic seed plants and may actually stimulate a variety of organisms (Moyle 1949). Certain algae are killed by 0.04 p.p.m. cupric ion while others withstand up to 100 p.p.m. *Mycobacterium tuberculosis* appears most sensitive among the bacteria, 10 p.p.m. of copper being inhibitive. For *Escherichia coli* the inhibiting concentration is 100

[1] Published as Technical Paper No. 716 with the approval of the Director of Agricultural Experiment Station. Joint contribution from the Department of Bacteriology and the Department of Fish and Game Management.

[2] Graduate student. Present address, U. S. Fish and Wildlife Service, Tule Lake Refuge, Tule Lake, California.

[3] Bacteriologist.

p.p.m.; for *Staphylococcus citreus* it is 1,000 p.p.m. (McCulloch 1945; Porter 1947). Although copper compounds are used extensively as fungicides, relatively high concentrations are required. Some common molds withstand several thousand p.p.m., and certain species of *Penicillium* and other fungi have been reported growing solutions saturated with copper sulfate. For higher plants about 0.1 p.p.m. Cu is optimum in solution cultures, while 5 to 10 p.p.m. are generally herbicidal.

The copper requirements for growth of *Spirodella polyrrhiza* are of the order of one part in 10 billion, and one part per billion is toxic in the absence of iron or manganese (Saeger 1937). This toxicity is overcome by addition of 500 p.p.b. of iron. A comparable counteraction of toxicity of copper was observed by Lewis (1942): in a synthetic medium 760 p.p.b. iodine prevented inhibition of *Azotobacter agile* by 200 to 400 p.p.b. copper.

Higher plants may show copper deficiency symptoms on certain soils, even in the presence of much total copper. Such soils are usually high in organic matter which ties up the copper and they may be treated with relatively large doses of copper salts to improve plant growth. Sandy soils low in copper also respond to applications of its compounds but the additions must be light; since the supply of humus is low, the "buffering capacity" for copper ions is correspondingly low and a toxic limit is easily attained. Effects of organic matter on availability of copper may well depend upon its origin and extent of decomposition. While peat humus shows high retentive power for copper, it has been found that soluble constituents of alfalfa and oat straw, acting presumably on copper-organic complexes, can increase the amount of copper extractable from soils with certain salt solutions (Hurwitz 1948).

Copper deficiency diseases of animals are often associated with soils and foodstuffs deficient in copper. Above optimum concentrations, copper salts become poisonous to animal as well as to plant life. Copper sulfate accumulations in bottom mud have been responsible for destruction of clams, worms, and insect larvae (Lackey 1949; Moyle 1949).

In some cases the effects of copper salts are indirect, or may be due to the anion. For example, the decay of algae killed by copper sulfate may so extensively reduce the supply of dissolved oxygen that fish die by asphyxiation rather than by copper poisoning. Under anaerobic conditions, sulfate is utilized by sulfate reducing bacteria, giving rise to hydrogen sulfide, which is a strong reducing agent and highly toxic to many organisms. Beneficial effects of copper in some cases may be due to its precipitation of sulfide. The addition of copper sulfate to certain peat soils coagulates the humus colloids, thus improving physical conditions and leading to more rapid nitrogen transformations and better crops. On the other hand, enhanced growth of plants following application of copper sulfate to the soil is often a response to sulfur fertilization.

Experimental

In view of the probable significance of bacteria in lake productivity, the present investigation was made to determine any correlation between numbers of bacteria and copper concentration in bottom samples from treated and control areas of Siltcoos and Tahkenitch Lakes, located on the Oregon coast a few miles south of Siuslaw Bay and emptying by short streams into the Pacific Ocean. Three samples from different treated areas and a control from an untreated area were taken from each lake with an Ekman dredge. The copper sulfate had been applied in several doses during the growing season approximately two years previous to sampling. Control was only temporary; at the time of sampling, the weed was abundant on treated as well as on control sites although the latter were more fringed with tules (*Scirpus* sp.). Areas treated ranged in size from 0.8 to 9.5 acres and extended from shore to depths as great as 10 feet in some cases. The

TABLE I. *Plate counts, copper, total carbon and nitrogen in lake bottom samples*

Sample	Nominal total copper treatment		pH	Bacterial plate count (numbers per gram)	Total copper in sample as Cu (p.p.m.)	Total carbon (percent)	Kjeldahl nitrogen (percent)	C/N ratio
	$CuSO_4.5H_2O$ (p.p.m.)	Cu (p.p.m.)						
Siltcoos Lake								
1	25	6.5	5.5	2,850,000	19	10.40	0.05	208
2	25	6.5	5.6	2,920,000	11	8.55	0.47	18
3	11	2.8	5.7	2,740,000	27	11.95	0.31	39
4	0	0.0	6.1	300,000,000	7	0.74	0.03	25
Tahkenitch Lake								
5	20	5.2	5.3	142,000	28	12.15	0.79	15
6	20	5.2	5.5	1,520,000	12	12.98	0.63	21
7	30	7.8	5.6	250,000	19	14.35	0.04	359
8	0	0.0	6.4	12,200,000	4	1.10	0.05	22

areas were so located that diffusion currents would be minimized by natural barriers such as weed banks and channels. Dosages, applied in part from towed sacks of blue vitriol and in part by throwing the crystals into water so they would fall to root zones, were designed to give concentration of 5 to 10 p.p.m. $CuSO_4 \cdot 5H_2O$ in the estimated volumes treated. Nominal total applications for the season ranged from 11 to 30 p.p.m. as shown in Table I. Actual concentrations were not determined.

The dredged samples were placed in sterile wide mouth jars with plastic lids and on the same day were brought to the laboratory for analysis. Determinations of pH were made in 1 : 5 suspensions of the samples, dry basis, in distilled water, using a glass electrode. Numbers of bacteria in the wet samples were determined from triplicate plates representing 1/1,000 to 1/100,000,000 dilutions prepared from 5 gram samples. All plates were poured with nutrient agar and incubated at 21° C. for 7 days. Counts were made on plates showing 100 to 300 colonies. Results, calculated on the dry basis, are presented in Table I.

For chemical analysis, subsamples were air dried, and ground with a porcelain mortar and pestle to pass a 60 mesh sieve. Copper was determined by the diethyldithiocarbamate method as outlined by the A.O.A.C. (1945). All glassware was cleaned with hot nitric acid. Distilled water, nitric acid, and ammonium hydroxide were purified by redistillation in Pyrex apparatus. Other reagents were purified as required, and blanks were run with all samples. Macro wet combustion was used for preparation of samples, $HClO_4$ being the final oxidizing agent. Copper was isolated from the digest as the dithizone complex, converted to the diethyldithiocarbamate, and estimated colorimetrically at 440 mμ with a Beckman "B" spectrophotometer.

Total carbon was determined by dry combustion, using A.O.A.C. (1945) procedure. A semi-micro Kjeldahl method with 0.500 to 4.000 gram samples was used for total nitrogen, the distilled ammonia being absorbed in saturated boric acid and titrated directly with N/70 H_2SO_4 in the presence of the bromcresol green-methyl red mixed indicator proposed by Ma and Zuazaga (1942).

The analytical data presented are compiled from duplicate determinations which showed good agreement in all cases. Variations from the average values per gram were within the following limits: for Cu, 0.5 μg; C, 0.6 mg; N, 0.2 mg.

RESULTS

Results are presented in Table I. The copper concentrations found in the bottom samples do not correspond to the nominal

treatments; this may be attributed in part to water currents and depth differences, and in part to additional treatments of unknown extent by resort operators in the area. The concentrations are low in comparison with 60 to 174 p.p.m. reported for some Oregon soils by Wood (1945). Labish peat soil, which from the standpoint of total organic matter is most comparable with the lake samples, showed the lowest amount. Data for other soils from various regions of the United States range from 5 to 140 p.p.m. (Holmes 1943; Manns and Russell 1934). Different soils and soil horizons vary widely in total copper, due particularly to differences in clay and organic matter content. Bottom mud of certain Wisconsin lakes have shown 18 to 1093 p.p.m. copper after a long history of treatment with copper sulfates; without treatment, the range was 32 to 135 p.p.m. (Moyle 1949).

The total carbon is consistent with the physical characters of the samples when dry. The controls appear to be almost pure sand, light gray to yellowish gray in color. Bottom material from treated areas is darker, feels less sandy and appears almost black and colloidal when wet; high total carbon in these is the result of deposition of the killed weeds. Comparative values quoted by Waksman (1938) show for almost pure sea sand 0.34 per cent carbon and 0.027 per cent nitrogen, while for a typical lake bottom the corresponding values are 7.08 and 0.69 percent. Some water humus samples contained 45 to 54 percent carbon and 1.46 to 4.23 percent nitrogen. Analyses of certain foreign lake muds show a range of 7.9 to 45.3 percent carbon with C/N ratios of 5.6 to 11.2 (Waksman 1941). Nitrogen in samples 1 and 7 is atypically low in proportion to the organic content; the extremely wide C/N ratios are characteristic of woody material or of fresh plant material low in nitrogen, but such explanation apparently does not apply to these samples. Values shown for the other C/N ratios are consistent in that they are typical of organic matter in intermediate and advanced stages of decomposition leading to humus formation.

Fresh samples of the water weed, cut off two or three feet above the crown, were found to average 54.10 percent carbon and 4.75 percent nitrogen, dry basis, with but slight differences between several samples from the two lakes.[4] The corresponding C/N ratio of 11.4 is exceptionally narrow for fresh plant substance; this may be due partly to harvesting only the upper, more actively growing portions of the plants, and partly to the apparent absence of reserve carbohydrate in *Anacharis densa*. It is apparent from Table I that humification of this material, which is the main source of the lake organic matter, widened the C/N ratio. This is in marked contrast with the narrowed C/N ratio that results from decomposition of ordinary plant residues.

The numbers of bacteria are much lower, except in the controls, than would be expected from the organic matter present. While the control sample from Tahkenitch Lake shows a count comparable to a soil with a similar organic content, the Siltcoos control is comparatively high. Considerably lower numbers were found by Henrici and McCoy (1938). In a study of shoreward distribution of bottom bacteria in the upper 18 cm. of the bed of Lake Mendota, they obtained counts of 35,650 to 836,900 per cc. In bay mud under 1 and 2 meters of water in another lake they found 126,100,000 and 1,013,400 bacteria per cc.

No systematic study was made of bacteria from different colonies on the plates. Examination of representative colonies indicated that cocci and gram-negative rods were common while spore formers were rare. There was little difference between samples in types of colonies and their proportions on the plates.

[4] Samples collected and analyzed by Franklin D. Aldrich, Graduate Research Assistant, Department of Botany and Plant Pathology.

Discussion

While the results of the limited study presented here seem to indicate that the copper treatments had an inhibiting effect on bacteria in the lake bottoms, the lack of data on other factors probably concerned becomes evident when interpretations are attempted. Figure 1 indicates that in the bottom samples from Siltcoos and Tahkenitch Lakes the numbers of bacteria according to plate counts were greater as copper concentration decreased, although the inverse relationship was not proportional. This apparent inhibiting effect of the copper is more striking when considered in connection with the total carbon, which multiplied by 1.7 gives a close approximation of the organic matter present. As a general rule, bacterial numbers increase with organic matter in sediments as well as in soils.

On the basis of organic matter alone, largest counts would be expected in samples 3 and 7; however these as well as the other samples similarly high in total carbon gave counts exceptionally low in comparison with the controls. Decomposition, and to some extent bacterial numbers, can be limited by an unfavorable C/N ratio, even though the organic matter is abundant. If the ratio is very wide, as in samples 1 and 7, the low proportion of nitrogen is limiting. A narrow ratio, as in samples 2 and 5, indicates extensive decomposition has already occurred and that the remaining organic material is resistant. A ratio of approximately 20/1 is optimum for decomposition in soils while 40/1 is more favorable for maximum activity by a

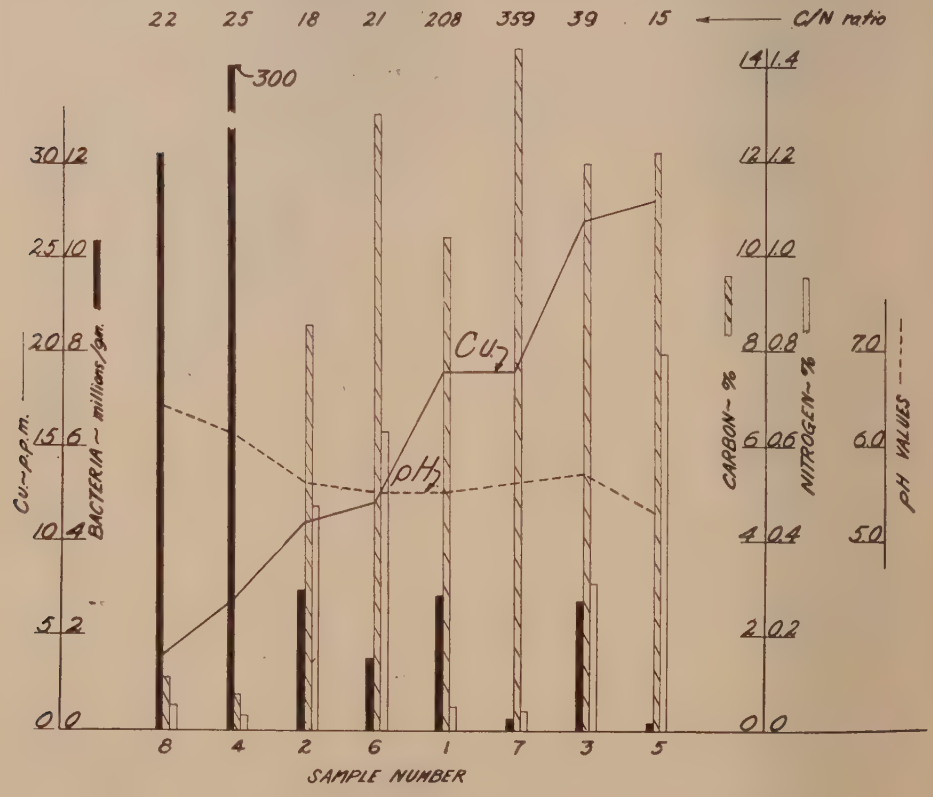

Fig. 1. Bacteria, copper, carbon, nitrogen, and pH in lake bottom samples.

mixed bacterial flora under aerobic conditions in water (Bollen 1951). Despite the retarding effects of an unfavorable C/N ratio on rate of decomposition, it is unlikely that this factor alone would account for the much smaller plate counts from samples having an abundance of organic matter. Although nitrogen starvation or resistance of substrate would slow down their rate of action, relatively large numbers of live bacteria could still be present.

Since copper availability increases with acidity, the pH values shown in Table I may be significant. On the basis of hydrogen-ion concentration, the samples showing inhibiting effects of copper were from 2.5 to 11 times as acid as the controls. Possibly more or less of the added copper sulfate was bound by organic matter or precipitated as carbonate, although the lake water is not hard. In either case, the acid reaction of the environment and the carbon dioxide generated by organic decomposition in the bottom mud would be likely to bring some copper back into solution. It is unlikely that the pH differences *per se*, being within the growth range of most saprophytic bacteria, could account for the differences in bacterial numbers.

From these considerations and from Figure 1 which emphasizes the absence of correlation between plate counts and carbon, nitrogen and C/N ratio, it appears that the inverse relationship between copper concentrations and plate counts points to an inhibiting effect of copper on bacteria in the samples containing 11 to 30 p.p.m.

This conclusion is difficult to reconcile with the large numbers of bacteria found to occur in soils containing 5 to 10 times as much total copper as was found in the bottom samples. Earlier investigations [5] in our laboratory showed that five samples of Labish peat soil, which contains 60 p.p.m. total copper, gave an average plate count of 84,667,000 on sodium albuminate agar; pH of the peat was 5.9 and the moisture was 51 percent or one-fourth saturation. Olympic silty clay loam soil, with 174 p.p.m. total copper, gave a count of 4,323,000 at approximately 50 percent saturation and pH 6.2. Difference in the counts for these two soils is attributable primarily to the difference in organic matter content.

Examples of stimulations resulting from additions of copper salts to soils and sea water also are at variance with the inhibition observed for the lake bottom samples. A study of some Olympic silty clay loam soil that had been used in the greenhouse to determine plant response to copper salts revealed that molds as well as bacteria were more numerous where 8 to 20 p.p.m. Cu as chloride or sulfate had been added. Although *Azotobacter* populations were stimulated, *Streptomyces* counts were decreased. With several muck soils Turk (1939) found that while $CuSO_4 \cdot 5H_2O$ at 50 and 100 pounds per acre (*ca.* 20 and 40 p.p.m. Cu) had no pronounced effect on CO_2 production and that it retarded rather than stimulated nitrification, it increased bacterial and fungal numbers in samples treated with 0-8-24 fertilizer.

Inhibiting effects of cupric ion may involve oligodynamic action, adsorption at cell surfaces, and inactivation of the sulfhydryl groups (-SH) or metal ion centers in certain enzyme systems. For bacteria at least, the effect is generally more inhibitory than lethal. Since copper exerts a synergistic effect on lethal action of hydrogen peroxide, the formation of peroxides may account for some of the bactericidal or marked bacteriostatic effects of copper in the presence of dissolved oxygen (Rahn 1945). Aeration of sewage is much more effective in the presence of Cu in suppressing putrescibility and numbers of bacteria (Cambosu, 1950). Similar action apparently does not occur or is not effective generally in soils, which are more or less well aerated, or in sea water, in which it has been observed that copper sulfate additions increased numbers of bacteria as well as dissolvd oxygen con-

[5] Unpublished.

sumption (Waksman *et al.* 1943). Surveys by the Oregon State Game Commission have shown that water immediately above the bottom of weed-infested areas of Siltcoos and Tahkenitch Lakes contains 7 to 8 p.p.m. dissolved oxygen. In view of this and the abundance of organic matter present, the peroxide theory seems applicable to the inhibiting effects of copper observed in the bottom samples from these lakes. However, this must be reconciled with the anaerobic conditions that must exist even slightly below the surface of the bottom deposits, with the reported action of copper in promoting anaerobic oxidation (Arnon 1937) and with the apparent lack of appreciable binding of the copper by the organic matter. It is possible that more or less aeration of the samples during collection and laboratory manipulation contributed to the effects observed.

Stimulating and inhibiting effects of copper are probably not attributable to copper *per se* but rather to available copper and the ratio of copper ions to other ions, such as those of iron, manganese and iodine, that may enter competitively or synergistically into certain oxidation-reduction systems. Total copper analyses do not indicate copper availability or its biological activity. Availability is determined by composition, pH, and physical properties of the soil or other medium; activity is determined largely by species of organism and probably also by concentrations of dissolved oxygen (Rahn 1945) and certain minor elements which may replace, antagonize, supplement, or otherwise interact with copper ions in redox systems. Since reactions of this nature are involved it becomes necessary to know the pH and dissolved oxygen concentration, and, where feasible, the oxidation-reduction potential. This is particularly true where comparisons are to be made of dissimilar systems involving mixed microflora and different environmental conditions. Data on the supply of organic matter and its C/N ratio are also essential. Certainly these are minimum requirements. Definition and determination of available and fixed copper by some appropriate procedure are desirable. Lack of any of this information for consideration with other experimental data on stimulating or inhibiting influences of copper often leads to speculation rather than to adequate interpretation of results.

Limitations of the present investigation are recognized. It is reported not only to call attention to the evident copper inhibition of a mixed bacterial population, but also to emphasize the array of factors which must be considered in such investigations.

Summary

It was found that residual copper from copper sulfate weed treatment in two Oregon coastal lakes effectively decreased the numbers of bacteria in bottom samples taken two years later. This inhibition was apparently caused by 11 to 30 p.p.m. total copper, and occurred in the presence of a large amount of organic matter. Controls containing 4 to 7 p.p.m. copper gave much higher counts although the organic content was low. The results are graphically summarized in Figure 1.

The results appear anomalous on considering the relatively low toxicity of copper for bacteria in general, and taking into account the tendency for organic matter to bind copper ions. These and other associated factors are discussed. The need for complete coordinate data on all such factors in studies on biological effects of copper is emphasized.

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THE GROWTH OF THE CLAM *MYA ARENARIA* AS AFFECTED BY THE SUBSTRATUM

EMERY F. SWAN [1]

Oceanographic Laboratories, University of Washington, Friday Harbor, Washington

INTRODUCTION

It has often been observed that the clam *Mya arenaria* L. grows faster and produces shells lighter in weight in sand than in mud or gravel. Belding (1916) doubts that this is a direct effect of the soil. However, the investigators in Maine apparently consider the soil an important factor in clam production (Spinney 1907, Dow and Wallace 1950), and Newcombe (1935) has demonstrated the limiting effect of shifting sand and silt-covered soft mud upon the growth of the clam. Loosanoff and Tommers (1948) have shown, at least for the area of their study, that suspended silt in the water reduces the rate of feeding by oysters, an observation suggesting needed work on clams.

It is the purpose of the present paper to report a single experiment which suggests a marked direct effect of the soil upon the growth rate, shell weight and relative linear dimensions of *Mya arenaria*. Because the number of clams studied was small, the results should not be considered conclusive but rather should serve as a stimulus to those who are able to carry on similar work on a larger scale.

The writer wishes to acknowledge State of Washington funds for medical and biological research for financial aid to this investigation.

EXPERIMENT

The writer (Swan 1952) has reported populations of *Mya arenaria* living only a few miles apart as having average shell weights for comparable lengths differing by roughly 30 per cent. One of the readily observable differences between the two places, Argyle Lagoon and Garrison Bay (both on the shores of San Juan Island, Washington), is the nature of the soil. In Argyle Lagoon it varies from a slightly muddy sand to a sand and fine gravel mixture, whereas at Garrison Bay it is a compact mud-gravel-shell mixture.

Four open-topped plywood boxes (24 inches long, 12 inches wide and 12 inches deep) were sunk into the sand of a level portion of Argyle Lagoon with their tops flush with the level of the surrounding sand. Their arrangement was such that there were no obvious environmental differences among their positions. Two of these were filled with local sand, and two with the mud-gravel-shell mixture from Garrison Bay where the heavier-shelled clams had been found.

On April 2, 1950, clams were collected from Argyle Lagoon. These were sorted, measured, and marked, and until replanted kept in the laboratory in running sea water.

On April 5, five each of five different length groups were planted in each of the four boxes. Before the first month had passed sand had washed over all the boxes so that the interface with the water at high tide was thereafter quite similar, but the soil in which the clams were buried was different. On March 28, 1951, these clams were dug and measured.

From the same original collection of clams, groups of two sizes were saved and divided equally between two similar boxes placed side by side in Garrison Bay—one filled with Argyle Lagoon sand and the other with the local Garrison Bay mud-gravel-shell mixture. Here it was some time (not recorded) before the surfaces of the two boxes were comparable. The mortality was higher and the results less conclusive, but for completeness these are also recorded. These clams were

[1] Present address: University of New Hampshire, Durham, New Hampshire.

planted April 7, 1950, and dug March 30, 1951.

Results

As can be seen from Table I, the clams grown in sand averaged roughly twice the gain in length of those in the mud-gravel-shell mixture and had shells of appreciably lighter weight and of proportionally smaller width and thickness.

Table I shows that the amount of growth within the groups varied greatly. Whether this is due chiefly to inherited variations, the past history of the individuals, or to differences in the individual clam's environment remains an open question. In a few instances the slow growing individuals of a group were obviously clams that were stunted before they were transplanted (*cf.* Needler and Ingalls 1944).

For both the series grown in the sand and the series grown in the mud-gravel-shell mixture the shell weights were consistently lower than would be expected on the basis of the previously reported data (Swan 1952). In order to find out whether the length-shell weight relations were appreciably different for the time at which the experimental clams were dug from the time these relations had previously been determined (Swan 1952), and in order to determine if the sand of Argyle Lagoon produced clams having the same average indices as large collections taken from the Lagoon as a whole (as was done in 1949), three new series of clams were dug (April 6–9, 1951). One group was taken within a radius of 15 feet from the experimental boxes in the sand in Argyle Lagoon, another from the gravel some 50 yards east in the Lagoon, and the third

Table I. *Data in millimeters and grams indicating effect of initial length and nature of sou upon growth rate, shell shape and shell weight of* Mya arenaria

Original length		No.*	Final length		Mean % increase in length	Final mean width	Final mean thickness	Final mean shell wt.
Mean	Range		Mean	Range				
Argyle Lagoon—sand								
15.6	13.4–17.2	5/10	46.3	43.2–51.7	197	27.0	15.1	2.57
25.1	22.7–27.5	8/10	49.4	38.8–59.3	97	28.9	16.8	3.44
40.0	38.5–42.1	10/10	59.9	51.9–65.9	50	35.5	21.4	6.74
55.7	53.0–57.2	9/10	65.2	55.7–72.8	17	38.8	24.9	10.96
71.4	67.4–75.2	10/10	73.5	69.1–82.3	3	44.3	28.4	17.57
Garrison Bay—sand								
28.0	25.7–29.1	4/7	64.6	56.7–77.9	131	37.8	22.2	7.61
39.0	35.6–41.6	0/4	—	—	—	—	—	—
Argyle Lagoon—mud-gravel-shell								
15.6	14.6–16.8	10/10	32.1	23.4–37.8	106	20.0	11.8	1.46
25.1	23.5–26.2	10/10	46.9	40.2–53.0	87	28.1	16.7	3.79
40.0	37.0–42.7	10/10	50.3	41.0–65.6	26	30.8	19.6	5.86
55.7	54.0–58.0	7/10	61.6	54.0–70.2	11	38.0	23.6	11.50
71.3	68.6–75.7	8/10	70.8	68.5–72.5	−0.7	40.3	27.7	16.54
Garrison Bay—mud-gravel-shell								
28.1	25.9–30.0	5/7	46.1	42.2–55.0	64	28.5	18.8	4.36
39.0	38.4–39.6	4/4	54.1	50.7–56.3	36	33.6	22.3	8.43

* Numerator = number recovered at end of experiment.
Denominator = number planted.

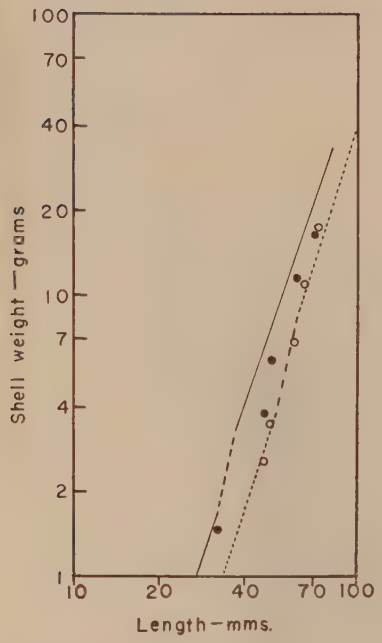

FIG. 1. Length to shell weight relations of *Mya arenaria*. The dotted lines represent relations found for naturally occurring population in the sand of Argyle Lagoon; the solid lines, the naturally occurring population in the mud-gravel-shell mixture of Garrison Bay. Connecting the two lines of each set the dashed lines cover the region of change in relationship. Hollow circles represent average relationships of the five size groups of experimental clams planted in sand of Argyle Lagoon. Solid circles represent those planted in the mud-gravel-shell mixture at Argyle Lagoon.

from the mud-gravel-shell mixture within 10 feet of the experimental boxes at Garrison Bay. The Garrison Bay collection fitted the previously determined relationship for that locality reasonably well. The clams from the sand at Argyle Lagoon had shells consistently lighter in weight, and those from the gravel had slightly heavier shells than indicated for the Lagoon as a whole.

In an earlier paper (Swan 1952) it was shown that in a log-log plot of shell weight against length for *Mya arenaria* the relationship was constant for lengths between approximately 10 mm. and a region of distinct shift in relationship, which often was found between 35 and 45 mm. in length. Then above this shift toward relatively heavier shells, the relationship is again nearly constant. The present study indicates that the clams growing in the sand of Argyle Lagoon have this shift at appreciably greater lengths than those obtained from the Lagoon as a whole (Swan 1952), whereas those collected from the gravel had the shift at lower values.

In Figure 1 the lines to the left indicate the average length to shell weight relations of naturally growing populations of spring-collected *Mya arenaria* L. in the portion of Garrison Bay studied. The lines to the right indicate the average length to shell weight relations of the same species collected at the same season from the sand adjacent to the experimental boxes in Argyle Lagoon. The hollow and solid circles plotted in the same figure represent the experimental clams growing in sand and mud-gravel-shell, respectively.

It can thus be seen that the clams planted in Argyle Lagoon sand did not vary in weight greatly from undisturbed individuals. The clams planted in the mud-gravel-shell mixture, however, were lighter in weight than native Garrison Bay populations. Obviously, prior to their being transplanted, their growth in Argyle Lagoon should have been such as to produce lighter shells. Thus one would expect the clams that were larger at the time of transplanting to show a greater effect of their previous environment. Certainly the point representing the smallest clams is closest to the line. The apparent great deviation of the next point may be because of a change in the position of the break in the relationship. Whether or not the others gradually increase in their distance from the line is not clear. Additional experiments are needed to clarify this effect.

The scatter of points for the dimensional relationships, as found in the previous study (Swan 1952) and also for the recently dug series, is such that a com-

parison of the experimentally planted clams with the "normal" dimensional ratios for the localities is difficult. Even so, the fact that the sandgrown clams tend toward lesser widths and thicknesses is obvious from Table I, especially for the smaller sizes where the experiment lasted for a greater portion of the clams' entire life to the end of the experiment.

Similar effects have been surmised in fossil brachiopods of the genus *Derbya* by Price (1920).

Discussion

That soil directly affects the linear growth rate, shell weight and linear dimensions of *Mya arenaria* L. is strongly suggested by the above experiment. If additional evidence substantiates this finding, the next question to be answered is, "In what manner does the substratum bring about this effect?". To date little evidence for the answer to this question is available, but the following factors should be considered as possibly affecting growth rate to which the shell weight and dimensional ratios are probably closely related:

1. Abrasion and chipping at the edges of the shell. Comparing series of clams dug from sand with those from nearby firmer soils makes it obvious that during their growth bits of shell often chipped off the edges of the clams from the compact soil, whereas those in the sand show nearly smooth edges and growth lines. One is tempted to wonder whether a clam's bodily growth is not limited by the rate at which it can permanently increase the size of its shell.

2. Positions of mantle edge in reference to shell. In extreme cases the mantle becomes detached from the shell for a considerable distance back from the edge, and between the old shell and the detached mantle new shell is formed. Such shells then have the appearance of a larger shell having grown within a smaller. Soil is often encased between the older part of the shell and the newer. One would expect such major repairs to slow down growth. Are they more frequent in firm substrata? No evidence is yet available. A more likely variation in mantle position would be the degree of outward expansion around the edge. If expanded to the maximum the shell-secreting cells would be spread out over a greater surface or be moved outward at a greater rate, and a more expansive but thinner new addition would be made to the shell. If the mantle were relatively contracted, a smaller area of shell of greater thickness would result from the same amount of secreted material. In a substratum of a loose nature it appears quite likely that the degree of mantle expansion would be greater than in a compact soil offering considerable resistance to increase in the size of the space occupied by the clam.

3. Irritation. Conklin (1913) has suggested that because of their more frequent irritation when expanded *Crepidula plano* growing on small shells probably fed less than those living on larger shells and hence grew more slowly even though plenty of food was available. In discussing the same irritation he mentions that individuals growing on small shells were unable fully to expand the mantle. Thus there is a possible interrelation between this irritation and the position of the mantle. Would not a clam in a hard-walled hole be in a situation somewhat comparable to the slipper shell on a small snail?

4. Energy needs. The amount of food required for the energy needed for the expansion of the shell in its hole and for the movement of the clam should be compared. Possibly, food that in the sand-dwelling clam is used for growth is in part used for added work by the dweller in more rigid surroundings.

5. Physico-chemical environment. The effect of the substratum on the clam's physico-chemical environment should not be disregarded. That the soil can contain materials toxic to the clam or of such a chemical nature as to dissolve its shell resulting in the clam's death has often been recognized (Kellogg 1905, Belding 1916,

Turner *et al.* 1948). The porosity of the soil with its effect on drainage and heat exchange at low tide should be considered in any complete study of this question.

6. Effect of position of clam in substratum upon shape of clam. Although no measurements have been taken, it is readily observed that the clams in the sand live at a greater depth than those in the mud-gravel-shell mixture. This obviously demands a greater habitual extension of the siphon. That this might stress the body of the clam so that it would tend to become relatively longer is a possibility, but this effect certainly does not account for anything approaching the entire difference in growth rate here observed.

Summary

1. An experiment wherein boxes of two different soils are sunk side by side in the same beach and stocked with *Mya arenaria* of comparable sizes is described.

2. After nearly a year's time there was found to be great individual variation in growth rate, but the average linear growth of clams in sand was found to be roughly double that of those planted in a compact mud-gravel-shell mixture.

3. Factors suggested as possibly responsible for the differences in growth rate include: differences in abrasion and chipping at the edge of the shell, usual position of the mantle edge in reference to the shell, external irritation and its effect on amount of feeding and position of mantle, relative amounts of food required for energy needs of clam, effects of the substratum upon the physico-chemical environment of the clam, and depth to which clam is buried.

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VEGETATION OF THE ANCIENT BEACHES ABOVE GREAT BEAR AND GREAT SLAVE LAKES

Alton A. Lindsey [1]

Department of Biological Sciences, Purdue University, Lafayette, Indiana

Introduction

The most striking geological feature of many islands and shores of Great Bear and Great Slave Lakes, Mackenzie District, Canada, is the system of abandoned beach lines. These originated during the recession of inland seas of post-Pleistocene time to the present positions of the two major lakes of northern Canada. Geologists have not reached agreement regarding the relative importance of postglacial uplift of the lake basin, drainage due to cutting down of the Great Bear and Mackenzie Rivers, or, in the case of the higher beaches, the possible influence of localized ice-dammed lakes. Cameron (1922a, 1922b) presented a geological account of postglacial history of the Great Slave Lake region. Some of the ancient beaches of this lake were characterized floristically by Raup (1946). In a report of an archaeological reconnaissance, MacNeish (1951) used the presence or absence of artifacts on beaches of various levels in determining the chronological sequence of the respective cultures. He includes a table correlating sites, beaches, and artifacts.

It was the writer's privilege in the summer of 1951 to serve as the botanist of the Canadian Arctic Permafrost Expedition sent to the Mackenzie Basin by the Purdue University School of Civil Engineering, under contract with the St. Paul Office, U. S. Army Corps of Engineers, and in cooperation with the National Research Council of Canada. The trip was a reconnaissance survey by airplane and boat, touching both north and south shores of Great Slave Lake, east to Artillery Lake and north to Warburton Bay, then following the 1,200 mile course of the Mackenzie River to the Arctic Ocean, with a side trip the full length of Great Bear Lake. This afforded an incidental opportunity to locate and examine a number of ancient beach formations, both from the air and on the ground, at several widely separated localities on the south and north shores of the two major lakes of northern Canada. (Fig. 1).

The highest beaches visited in this study are 700 feet above the present level of Great Slave Lake. Often single beach lines at the higher elevations show narrow zones of vegetation ranging from crutose rock lichens to white spruce cover.

Geological Description

Except on rather flat shores, where broad parallel ridge-tops scarcely differ perceptibly from nearby ones in elevation, beach ridges occur in series which are distinctly step-like. Each beach line shows a characteristic profile. Its steep slope faces lakeward. At the top of this slope, it breaks abruptly to a generally flat ridge-top which follows the contour. Where the general slope supporting the series of beaches is relatively steep, the ridge-tops are narrower than where the series occupies a gentle slope. Very narrow ones may show no flat surface, but consist of two slopes, a lakeward steep slope meeting a gentle rear slope. The latter forms a trough where it meets the

[1] The writer is grateful to Prof. K. B. Woods of the Purdue University Civil Engineering School who was in charge of the Canadian Arctic Permafrost Expedition; to Mr. A. E. Porsild and Dr. I. M. Lamb of the Canadian National Museum for verifying identifications of the vascular plants, and determining lichen species, respectively; and to Dr. Ira C. Brown of the Canadian Geological Survey. Plant specimens are in the herbaria of Purdue University and the National Museum of Canada. Permission to publish was granted by the Office of the Chief of Engineers, U. S. Army.

base of the steep declivity of the next higher beach.

In a beach ridge of the common form, the back edge of the flat top very gradually gives over to a gentle slope which drops down to form a depression as much as three feet below its ridge top. From the bottom, the steep lakeward slope of the next higher ridge begins. The differing water relations and amounts of soil, humus, and litter accumulation in these situations bring to bear the influence of physiography upon the vegetational pattern.

The texture of the materials constituting the elevated beaches of today correlates with general topography. Likewise, the profile showing the surface form of an individual beach is correlated with its texture. Steep topographic situations support only boulder beaches, since fine materials were washed out during beach formation on steep slopes. Consequently, boulder beaches generally have steeper lakeward slopes and narrower tops, and thus are narrower over all, than beaches of finer materials. The finer the texture of beach materials, the shallower is the depression behind the ridge-tops. Exceptions to this last statement were noted

FIG. 1. Map showing locations of beach ridge areas visited in the Northwest Territories, Canada. A. Hornby Bay (upper dot) and Norrie Bay (lower dot), McTavish Arm, Great Bear Lake. B. Et-then Island, Great Slave Lake. C. Hay River settlement.

FIG. 2. Recently formed series of bare beach ridges on a small island in Great Bear Lake south of Hornby Bay. Even the oldest of these support little cover except lichens. Rhyolite porphyry rock on the left developed into ridges, whereas none formed on the dark columnar andesite and trachyte on the right.

between certain sand ridge-tops that are exceptionally far apart.

Sand beaches have broad ridge-tops and are situated near the present lake level where the shores slope gently. Those examined are not more than 200 feet in elevation above Great Slave Lake or Great Bear Lake, although Dr. I. C. Brown (private communication, 1951) writes of seeing "a fine sand beach right at the top of a steep hill some 1,000 feet above Great Slave Lake and 200 feet above the surrounding country. Certainly most of the sandy beaches, that I know of, are close to lake level." The lowest and most recently formed of the old beaches are not necessarily of fine material. Those occurring on steep shores are of boulders.

The heavy ice armor of these lakes favors prominent beach ridges. The chief factor in the formation of at least the coarser ridges is ice-shove. These ridges often lack flat tops; the steep front slope meets the gentle rear slope directly, which indicates that ice-shove was responsible. The writer's conclusion on the role of ice action in spring in the formation of beach ridges was reached independently, but parallels the previous concept of Tyrell (1910) and accords with Brown's recent observations. In private communication, Brown stated, ". . . you attribute the coarser steeper ridges to ice-shove. In 1949 I saw some of these higher ridges actually shoved up by wind-blown ice sheets and apparently when they were shoved above the normal wave limit they were preserved while lower ones were reworked and flattened by later wave action." This sort of upbuilding should make it possible for the numerous strand lines only a few feet apart (Fig. 2) to have developed during continuous regular, rather than intermittent, withdrawal of the lake from these beaches.

Sand beach lines differ from sand dunes in that their ridge-tops are continuous for long distances, follow the contour, are flatter in profile, generally parallel each other quite regularly, form a series ascending in elevations from the lake inland, and may contain more and larger gravel than dunes. Where not well-stabilized by vegetation, sand beach ridges may be reworked by wind without losing the general character of old beaches. There is a tendency in these cases for a

concentration of the wind resistant gravel on the surface, as a sort of crust of coarser material. Broad sandy beach ridges at low elevations grade into broader formations which should probably be termed lacustrine terraces. Sand formations of this nature were seen from the air by other members of the expedition on the north and south shores of Great Bear Lake; these are not included in the following treatment.

Location of Stations

The map (Fig. 1) shows the location of most of the beach ridges examined. Those under the most severe climate are at the arctic timberline on the hill at the north shore of the northeast point of Hornby Bay, McTavish Arm, Great Bear Lake. Their position is 66° 41′ N. Lat., 117° 35′ W. Long. Well-developed beach ridges, including materials of boulder, cobble, gravel, and sand texture classes, extend for at least ten miles westward from the extreme northeast finger of Hornby Bay. Their vertical limit is approximately 600 feet above the lake.

On the northwest side of Norrie Bay, McTavish Arm, beach lines ranging from boulder to gravel occur at 66° 28′ N. Lat., 117° 34′ W. Long. Other conspicuous ones were seen on both sides of the entrance to Western Channel and on several low, small treeless islands north of that point in McTavish Arm (Fig. 2). In the report that accompanies a Geological Survey map, Feniak (1949) comments on the profusion of beach ridges in Norrie and Hornby Bays.

Et-then Island near the base of the large northeast arm of Great Slave Lake (62° 15′ N. Lat., 111° 45′ W. Long.) shows quite diverse surface geology for a small area of the Pre-Cambrian Shield. Its intermediate elevations have inconspicuous beach lines derived from sandstone. Northward, at higher elevations, occur very step-like beach ridges in embayments in the steep diorite escarpment which caps the island. From preliminary study of airphotos of a scale of 1:31,000 prior to any field experience with high beaches, it was judged that these relatively treeless beaches were of sand, because of their very light tone on the prints. They proved to be of dark diorite boulders so densely covered with *Parmelia* and other lichens as to have a light gray appearance.

From some of the ridge series in breaks of the cliff, boulder beaches continue stepwise to the high points of the island. These are very evident as beaches on even the small-scale airphotos available. The continuity of some of the oldest ridges has been broken by erosion so that they are recognizable as beaches from airphotos by the vegetational arrangement, but not from ground observation.

Near the lake level along the south shore of Great Slave Lake, extensive beach-line terrain is seen from the air about Hay River. This settlement lies at 60° 50′ N. Lat., 115° 45′ W. Long., at the northern terminus of the road from Edmonton. The two groups of old ridges examined on the ground were 10 miles west of the mouth of Hay River, and 15–18 miles south of town along the road. These are sand ridges on low land.

Methods

Two methods of photographic sampling were used for quantitative studies. Numerical abundance per acre for the white spruce forest was based upon available airphotos. Three zones of low-growing vegetation were analyzed by enlargement of 4″ × 5″ vertical ground photographs taken, with accompanying notes and specimens, during the field work.

Airphoto sample plots were located in the 237 square mile MacAlpine Channel Map-area because a detailed geological map (Feniak 1949) is available, and the several excellent beach series at Norrie Bay are included. The Purdue Airphoto Laboratory loaned 132 airphoto contact prints (8½″ × 8½″), from which a large-scale mosaic of the entire map-area was assembled by stapling the prints on a large

beaverboard. Bedrock types were delimited on this with a glass-marking pencil, following the geological map. After unassembling of the marked mosaic, stereopairs were studied with a pocket stereoscope. Fifteen 4-acre plots four times as long as wide (i.e., four acres in a line) were marked out under stereo, confining all the sample area to beach terrain occupying general slopes of 2 to 9 per cent. Per cent of slope was calculated from parallax measurements obtained from stereopairs by the Abrams Height Finder, Model HF-2.

At the 1/28,000 scale of these airphotos, the twofold magnification by the stereoscope does not permit counting individual spruces. Counts were made from a single print under the tenfold magnification of a binocular dissecting microscope, by pricking each tree with a needle as counted. While this method would not be feasible for a closed stand of spruce, in the widely spaced beach-line cover, the black, pointed shadows of individual trees contrast well with the light lichen cover of the ridgetops. The main limitation to accurate counts is that an arbitrary size standard must be held in mind. Below this size, approximately six feet tall, trees are not counted, because many smaller trees are too small or too crowded to cast characteristic shadows, thus they are not distinguishable from shrubby species. The particular prints selected for microscopic counting were those in sharpest focus; often one print of a stereopair is considerably sharper than the other.

In the part of the northern transition spruce forest studied, species identification from airphotos is no problem, since *Picea glauca* (white spruce) is the only tree of any vegetational importance on old beaches, and is the only species of gymnosperm with tree form that is present at all, except *Picea mariana* (black spruce) which is confined to muskegs. The data from the four-acre units on old beaches were subjected to analysis of variance. The method and number of plots used were shown statistically to yield a satisfactory degree of accuracy.

An additional 45 non-beach plots of the same size on four different bedrock types were studied for comparison with beach tree stands and with each other.

For detailed analysis of the ground cover contributed by lichens and other low-growing plants, vertical ground photographs in color or monochrome were taken, together with notes and specimens from the photographed plots. The 4″ × 5″ panchromatic negatives were enlarged on 14″ × 11″ double weight paper, the outlines of the plant clumps or individuals were cut out with scissors, and these pieces sorted by genera, and, where possible, by species. The color photographs were projected in a dark room upon Marquette grade tag paper as images two feet in length, the boundaries of each plant unit traced, and all cut out and sorted. By both methods, the paper piles were weighed on an accurate balance, and cover percentages calculated. For vegetation in which all plants are nearly in the same plane, this is a highly accurate method for determining cover within the quadrats; the vegetation is worked out in great detail. It has the further advantage of conserving the limited and expensive time available in the field. The use of color film is slightly more accurate, since color facilitates recognition of the plants.

The beach vegetation will be considered under headings relating to the predominant vegetation type of the general region of the beach line series. The region of most severe climate will be discussed first.

Forest–Tundra Ecotone Region

The northernmost post-glacial beaches examined lie at the arctic timberline on the slope north of Hornby Bay, Great Bear Lake. This is by far the most extensive continuous area of boulder beaches observed. At elevations less than 300 feet above the lake, the *Picea glauca* forest is relatively dense both on the lower boulder strands and below them. On

FIG. 3. An edaphic timberline on coarse boulder beaches north of Hornby Bay, Great Bear Lake. Spruce stands occur also beyond the left edge of the photograph above the highest beach ridge. The climatic, non-beach timberline at this altitude is more than a mile farther north.

approximately the 300 foot contour (Fig. 3) is an abrupt edaphic timberline; only small scattered spruces occur on the higher beaches. However, above the highest beach occur large patches of timber. The general or climatic timberline on the upland occurs about 1.5 miles beyond the highest, northernmost beach ridge. Except for the spruce and *Betula papyrifera* (paper birch), all the ecologically important plants of this timberline community penetrate far north into the tundra. Thus the dominant dry-tundra species are those which also characterize the four non-tree zones of these beach lines.

As usual, the bedrock determines the lithology of the beaches. The lower ridges (Fig. 4) are of boulders of rusty-red, medium- to fine-grained, siliceous sandstone, averaging 14 by 10 by 3.5 inches. Just below the youngest beach, the white spruces average 50 feet in height and 13 inches d.b.h., while on the adjacent beaches they average only 19 feet tall. Below the beaches, paper birch occurs prominently with the spruce; in the beach troughs it is replaced by abundant ground birch (*Betula glandulosa*) from 3 to 6 feet in height, both under the spruce and as a tall shrub zone extending into the less mesic habitat bordering the line of trees.

The lichen zone on the ridge tops is largely composed of *Parmelia separata, P. centrifuga,* and especially *Umbilicaria* spp. The slightly more mesic zone of fruticose lichens has a closed cover of *Stereocaulon paschale, Cetraria nivalis, C. cucullata,* and *C. islandica.*

The higher beaches are composed of pebbles disintegrated from coarse arkosic conglomerate bedrock. The smoothly oval and spherical pebbles contrast with the rather angular rock fragments of most rocky or gravelly beaches; however, the water-worn nature was acquired before their cementing into conglomerate and not

by wave action on the post-glacial beaches. The relatively fine-texture of the gravel resulting from this peculiar origin counters somewhat the effects of the extreme climatic severity of the timberline beach series.

The xeric lichen zone on conglomerate appears identical with the corresponding zone on sandstone. The second lichen zone (*Stereocaulon–Cetraria–Cladonia*) shows greater variety on the conglomerate-derived gravel, including *Cladonia amaurocraea, C. mitis, Cornicularia divergens, Cetraria cucullata, C. islandica, C. nivalis,* and *Lecanora* sp.

Table I shows cover percentages for the xeric lichen zone (1), fruticose lichen zone (2), and low shrub zone (3) from combined quadrat data from Hornby and Norrie Bays. The table indicates considerable overlapping in species representation between zones 1 and 2, but the pronounced dominance of *Umbilicaria* in the former and *Stereocaulon* in the latter is revealed. Not included in the table are the *Betula glandulosa* zone (4) and the *Picea glauca* zone (5).

TABLE I. *Per cent cover in the first three zones on beach ridges of the forest-tundra ecotone, Hornby and Norrie Bays, Great Bear Lake. Zone 1, 5 quadrats (13.3 square feet each); zone 2, 2 quadrats; zone 3, 3 quadrats*

	Zone 1	Zone 2	Zone 3
Bare rock or thin crustose lichens	22.0	1.2	3.1
Umbilicaria spp.	52.8	0.4	0.1
Parmelia spp.	17.2	—	tr.
Cetraria spp.	0.4	13.9	20.6
Stereocaulon paschale	6.4	63.6	3.9
Cladonia spp.	1.2	4.3	—
Litter	—	7.4	25.2
Vaccinium vitis-idaea var. *minus*	—	4.5	6.2
Empetrum nigrum	—	—	3.6
Salix reticulata	—	—	15.2
Arctostaphylos uva-ursi	—	—	20.0
Betula glandulosa	—	4.7	—
Saxifraga tricuspidata	—	—	1.9
Grass	—	—	0.2

Twelve miles south of timberline and the beach ridges discussed above, the

FIG. 4. A Hornby Bay (left) beach line of coarse boulders covered by crustose and foliose lichens. The shrub clumps in the continuous depressions are *Betula glandulosa.* Beyond the man, the ridge curves to follow the contour.

FIG. 5. Foliose lichens (*Umbilicaria*, dark; *Parmelia*, light) and some fruticose lichens on the flat top of a cobble-gravel beach ridge at Norrie Bay, Great Bear Lake.

series on the northwest shore of Norrie Bay comprises at least 30 ridges of trachyte and andesite. The higher ones are gravelly in texture with 1 to 4 inch rocks which are somewhat water-worn. The dry ridge-tops show a close-clinging lichen cover (Fig. 5) largely of *Umbilicaria hyperborea, Parmelia separata, Cetraria hepatizon,* and *Rhizocarpon geographicum,* which produce a dark general tone. In the slightly moister habitat of zone 2, the dominant *Stereocaulon paschale* is accompanied by *Cetraria islandica, C. nivalis, C. Richardsonii, Cladonia alpestris, C. mitis,* and *Alectoria lanea.*

Both Hornby and Norrie Bay beach series show two shrub zones. The important shrubs in the low shrub community (Fig. 6, and Table I, zone 3) are *Arctostaphylos uva-ursi* (bearberry), *Salix reticulata,* and *Vaccinium vitis-idaea* var. *minus.* At Hornby Bay, bearberry was not seen on the sandstone beaches, but was abundant on ridges of conglomerate origin. *Juniperus communis* is occasional with bearberry at Norrie Bay but is absent at Hornby Bay. One lichen genus, *Cetraria,* covers 20.6 per cent of the low shrub quadrat areas; the distinctive coarse brown *C. Richardsonii* occupies 58 per cent of the *Cetraria* cover. *Betula glandulosa* and *Juniperus communis* are the only species of consequence in the tall shrub zone. Other shrubs are characteristic of the white spruce zone as understory species; the commonest of these are *Vaccinium uliginosum* and *Empetrum nigrum. Ledum decumbens, Salix planifolia,* and *S. glauca* var. *acutifolia* are characteristic of the moistest depressions between these beach ridges.

White spruce in the troughs at Norrie Bay average 7 inches d.b.h. (maximum 10 inches) and 52 feet tall (maximum 65 feet).

Fifteen four-acre airphoto plots were located on the rock type mapped as "tra-

chyte and andesite locally trachytic in nature" north and northwest of Norrie Bay and north of the eastern end of Western Channel. The aggregate area of the plots is 60 acres of exclusively beach deposited material. All the plots are situated on general slopes between 2 per cent and 9 per cent.

The number of trees counted per 4 acre plot ranged from 58 to 128. Analysis of variance showed the standard error of the mean of 87 trees to be ± 9. Since there is a probability of 95 per cent that the mean of 87 does not depart more than 9 from actuality, 22 is a close approximation to the mean number of white spruces per acre on the beach ridges near Norrie Bay.

Four distinct bedrock types in the same map-area were compared by 45 airphoto sample plots of 4 acres each, not located on beaches. Relatively level (less than 2 per cent slope) land, on exposed domes and ridge tops with much bare bedrock, provided a comparable habitat for all rock types. The open forest growth made counts possible from the 1/28,000 scale airphotos; more favorable sites often had stands too dense to use the method. Ten plots on trachyte and andesite averaged 58 trees per four acre plot. Fourteen plots on arkosic conglomerate averaged 39 trees per plot, while seven plots on granite averaged 5 trees each. Thirteen plots on rhyolite porphyry averaged 14 trees per plot.

Steep north-facing slopes have low stands, denser but seldom taller than those on level ridges and domes where the plots were placed. The tallest stands in the region occur along streams and on south-facing slopes. Four plots on rhyolite porphyry talus slopes of 18 to 22 per cent, facing south, averaged 132 trees (more than approximately 6 feet tall) per four-acre unit. The abundant reproduction on these south slopes above lakes made the count difficult. The best stand

FIG. 6. Patches of *Arctostaphylos uva-ursi* occupy the drier parts of the depressions between high beaches above Norrie Bay, Great Bear Lake, but not the still drier ridge tops of coarse gravel where foliose lichens predominate.

FIG. 7. Low oblique air view showing a short series of diorite boulder beaches 600 feet above Great Slave Lake, near the summit of Et-then island. Rock lichens contribute the light tone. The greater size and vigor of individual spruces in the ridge area, in contrast to trees below and above it, is due to protection from fire and less competition for water.

had 186 trees in the plot; yet the presence of many tall trees was more striking than the greater numbers.

BEACHES IN THE WHITE SPRUCE–PAPER BIRCH REGION

All the beach lines studied in the climatic zone dominated by stands of *Picea glauca* and *Betula papyrifera* are on Et-then Island, Great Slave Lake. This island is composed of three bedrock types. The low southwestern end, with abundant lakes and muskegs, is of red sandstone. The white and black spruce forest that prevails there has been very little affected by fires, but in the few burns trembling aspen (*Populus tremuloides*), not paper birch, has followed the fires. The sandstone base is overlain by many strata of coarse conglomerate. The latter supports white spruce, but has large areas opened by fires and now dominated by paper birch less than 15 ft. tall. Beach ridges are found on both the sandstone and conglomerate terrain, especially the latter, but on both they are difficult to trace. This is partly because of the uniform tree growth over the entire profile of the beaches. They are obscured even more by the prominent banding arrangement produced by the northeast dip of the conglomerate strata. The resulting series of low terraces brings about vegetational alternes, with dense white spruce cover and deep moss in the moist depressions. Open park-like spruce and light-colored *Cladonia* lichens characterize the dry ridges. The alternes produce a distinct pattern on 1/31,000 scale vertical airphotos. The beach ridges, which are not distinguishable on the airphotos, follow the contour, while the structural ridges do not, although sometimes they are not far from it. The exposed edges of the

eroding conglomerate strata show steeper, more abrupt faces, and more wavering or irregular lines than beach ridges.

All the conspicuous high beaches on Et-then Island are on the diorite sill (Fig. 7), or else are of coarse diorite boulders of the talus below the great escarpment. The latter is the most prominent scenic feature of Et-then; it runs northwest-southeast nearly across the island. Beach ridge series occur in each of six deep embayments where erosion has broken down the cliff. Figure 8 shows part of such a series. Above a series of 22 ridges in a large bay or notch of the cliff, 32 additional ones were counted in a continuous series on the slope of the diorite sill almost to the island's summit. The ridges are of angular, flattened boulders averaging about 13 inches long, except for a small series of low elevation sand ridges on the northeast slope. Evidence of strong ice shove in their formation is seen in many of these boulder ridges.

Most of the boulder ridges in the notch lack any trees, whereas the nearby sand ridges of the same ages and elevations on the slope on the other side of the divide support spruce at least in the troughs and often over the tops also.

No beaches of bare rock are found, since closely growing *Parmelia*-type lichens occur wherever larger plants are lacking. The lichens determine the color tone of these beaches as a light gray.

In the upper series of 32 boulder beaches, the width of each complete beach ridge was determined by pacing. These beaches ranged in width from 10 feet to 62 feet, averaging 33 feet. The vertical height of each ridge was estimated and found to range from 1 foot to 8 feet, with 3.8 feet the average height. The general slope on which these beach ridges lie is one of approximately 7°.

FIG. 8. One of the many embayments in the diorite sill that caps Et-then Island, Great Slave Lake. All of these embayments support series of coarse boulder beaches with sparse tree growth or none. Light foliose lichens of the *Parmelia* type produce a light tone.

A typical beach of the upper series shows a zonation from rock lichens on the top to spruce and paper birch in the troughs. On the dry ridge tops, the dominant lichens are several species of *Parmelia* mixed with *Umbilicaria angulata* and *U. papulosa.* The next, slightly less xeric, zone is characterized by a closed cover of fruticose lichens an inch to 2 inches in height. The rock is completely obscured by the living plants and litter derived from the lichens and nearby higher plants. The important dominants in this fruticose lichen zone are *Cetraria nivalis* and reindeer lichens (*Cladonia* spp.).

Nearer the trough is the zone of low shrubby plants, chiefly *Empetrum nigrum* and *Arctostaphylos uva-ursi.* This zone is usually only a few feet wide, bordering (and extending beneath) the line of trees in the trough. However, where it is more extensive due to the washing in of soil upon the highest beach ridges, *Juniperus horizontalis* is frequent and a few white spruce seedlings and saplings occur. Ground birch, the principal component of the shrub zone on beach ridges north of Great Bear Lake, is unusual on the Et-then beaches. The chamaephytes *Salix reticulata* and *Vaccinium uliginosum,* which are also important beach ridge shrubs in the more northerly locality, are absent from the Et-then beach ridges.

The last zone is represented by a narrow band, in fact, usually a single row, of *Picea glauca,* often accompanied or bordered by *Betula papyrifera.* On the diorite bedrock away from the beach ridges, paper birch is very abundant and trembling aspen is uncommon. The only site on diorite where aspen appears to thrive is among coarse blocky talus boulders below the diorite cliff. The trees are uniformly large, with an estimated average d.b.h. of 11 inches, and there is no evidence of fire or former spruce dominance on this site. On the beach ridges of the upper series, no aspen was encountered. Jack pine (*Pinus banksiana*) does not occur on any of the beaches of this island.

The tree zone may form a continuous line, or in the drier troughs it may be interrupted by the shrub community, or even by one or both of the lichen communities where the tree row is broken by a wide gap. Where the trees are very intermittent, spruce may occur in troughs where no soil is visible among the loose angular boulders. A slightly deeper trough, such as 3-feet instead of 2, confers a marked advantage for tree growth.

Most soil accumulation occurs on the highest beaches. This is due less to their greater age than to their finer, more gravelly texture and especially to the washing down of soil and litter from the bedrock areas adjacent to the highest beach. None of the boulder beaches on this island have developed a soil cover over all parts of the beach profile except by such accumulation of extrinsic materials from a non-beach substrate. In the troughs of these beaches, the white spruce is as much as 45 feet tall.

Several broad and widely spaced gravel or sand beaches less than 300 feet above the lake level have developed a thick organic soil over all. Beneath the dense spruce–paper birch cover of the troughs is good spruce reproduction, and the shrubs (*Ledum groenlandicum, Andromeda polifolia,* and *Alnus incana*) are more mesic ones than those on the higher beaches. *Larix laricina* (tamarack) occurs only in *Picea mariana–Dicranum bergeri* muskegs below the lowest beach deposit. The latter, 210 feet above the lake, is of sand containing large water-worn pebbles. It supports a normal uniform white spruce cover.

The spruces of the beach ridges are protected from the advance of forest fires by the treeless ridge-tops. In several areas such trees attain larger size than adjacent trees on diorite which had burned over. During one rather recent burn, the fire had stopped at the edge of the beach ridge area.

FIG. 9. Recent beach ridges of sand near Hay River, south shore of Great Slave Lake. Jack pine (left) occupies the ridge top, white spruce (right center) a north slope, trembling aspen (right) a south slope.

BEACHES IN WHITE SPRUCE–JACK PINE–ASPEN REGION

The strands in the flat land south and west of Hay River settlement are broad sand beaches very different in profile, texture, climate, and vegetation from those discussed above. At a point where bank erosion by Hay River had sectioned directly across the ridges and troughs, the material at the base of the cut is glacial drift of silty clay, with some boulders. Overlying the drift is lacustrine sand with fine gravel; beneath the ridge-tops this surface deposit is 15 feet deep, while beneath the depressions it is 5 feet.

In general, the profile is rather symmetrical, with flat tops, similar slopes on either side, and wide troughs from 2 to 10 feet below the ridges. The well-drained white sand of the ridge-tops (from 20 to 170 feet wide) is dominated by jack pine with aspen next in abundance. Figure 9 is a photograph of the trees of a ridge top and both slopes.

The chief ground cover on the ridge tops is *Cladonia mitis* covering about 72 per cent of the surface. Scattered *C. cornuta* is mixed with it, and patches of *Cetraria nivalis* 8 inches in diameter occupy 1.5 per cent. *Arctostaphylos uva-ursi* is the prevailing shrub (19 per cent), and *Vaccinium vitis-idaea* covers 8 per cent. Two per cent is bare, and the remainder is *Rosa acicularis, Equisetum arvense, Cornus canadensis,* and *Geocaulon lividum.* Litter and humus is 2 inches deep over the white sand. The dry ridge tops are quite susceptible to fires.

The south-facing slopes are dominated by white spruce, with aspen, jack pine, and *Populus tacamahaca.* The lakeward slope also may support white spruce aver-

aging 30 feet in height, but usually the jack pine or aspen continues down from the ridge. When aspen dominates on the north slopes, its shrubby understory is composed of *Juniperus horizontalis, Shepherdia canadensis,* and *Potentilla fruticosa.* Where white spruce dominates on either slope, *Ledum groenlandicum* is the abundant shrub, with *Empetrum nigrum* next, and the moss, *Hylocomium splendens,* is the only important member of the lowest stratum.

The troughs range in width from 35 to 390 feet. One type of vegetation in the broader troughs is ground birch muskeg, the birch (*Betula pumila* var. *glandulifera*) averaging 4 feet in height. *Salix glauca* and *S. serissima,* growing up to 4 feet tall, are subordinate to the birch. The principal moss under these shrubs is *Drepanocladus revolvens,* which grows rather sparsely. *Larix laricina,* averaging 35 feet tall, occurs in a marginal band in some birch muskegs while white spruce covers the higher ground. The other common type in troughs is represented by *Picea mariana* muskegs, which include also tamarack, ground birch, and willows.

Discussion

In the troughs of coarse beach ridges, soil has been derived more from windblown material, especially organic debris, from outside the beach series than by weathering of the beach boulders. Thus, the vegetational development in troughs is not a typical self-contained sere, but it retains the essential feature of succession —reaction by plants upon the habitat which is thus enabled to support more advanced life forms and communities. Although this appears superficially as a prisere, the presence of extrinsic soil and organic debris settled between the rocks confers the advantages of prior reactions and makes the sere, somewhat paradoxically, essentially a subsere.

In the boreal regions generally (Raup 1941) or in the timberline beach ridge series in particular, climatic instability or brevity of time for vegetational stabilization may make the occurrence of a true climatic climax questionable. Nevertheless, it is possible to recognize deductively a probable developmental sequence among the various communities within a limited area. At least the earlier stages can be differentiated even when seral progress is extremely slow and poor differentiation exists between the later stages and among the possible climaxes. The high boulder or gravel beaches represent relatively simple cases. The *Picea glauca* cover in the slightly moister depressions, whether an edaphic subclimax or in balance with the existing climate, is more advanced and less xerophytic than the shrub or rock lichen communities associated with it in the zonation from trough to beach crest.

The spruce trough community has developed north of Great Bear Lake in a very few millennia since lake recession; it is unlikely that this appeared fully developed as the first plant community to occupy its site. Such zoned vegetation grades into the unzoned vegetation on nearby beach ridges which support a continuous cover of forest over both tops and depressions. There is every indication of a successional relation from the uniformly treeless to the continuously forested beaches, involving significant changes to the substrate, such as peat deposition over the beach material, during successional advance.

The geologically brief post-lacustrine time span and the concurrent climatic changes may well have prevented stabilization of clearly differentiated boreal climaxes but plant succession has occurred on beach ridges without necessarily having yet produced final stages in balance with existing climates.

Summary

Postglacial beach deposits of Great Bear and Great Slave Lakes range in texture from sand to coarse boulders. To generalize, the boulder and gravel beaches exhibit an *Umbilicaria-Parmelia* successional stage on the xeric ridge-tops. This

is supplanted by a *Stereocaulon-Cetraria-Cladonia* community.

On the Great Bear Lake beaches near the arctic timberline, a low chamaephytic shrub stage precedes a taller phanerophytic shrub community. The highest stage, mainly occurring in troughs, has but one tree species, *Picea glauca*. At Norrie Bay, 66° 28′ N. Lat., the mean number of white spruces more than 6 feet tall is 87 ± 9 trees per four-acre plot, as determined from airphotos.

The boulder beaches at Et-then Island, Great Slave Lake, in the white spruce-paper birch vegetation region, show a single mixed shrub zone. The tree stage, while predominantly spruce, includes considerable *Betula papyrifera*.

The white spruce-jack pine-aspen type is general near Hay River on the south shore of Great Slave Lake. The broad sandy beach ridges support *Pinus banksiana* and *Populus tremuloides* on the well-drained ridge-tops. *Picea glauca* characterizes the gentle slopes. The vegetation of the depressions is rather variable; it is usually either birch muskeg (*Betula pumila* var. *glandulifera*) or *Picea mariana* muskeg.

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NOTES AND COMMENT

A METHOD OF MOUNTING THERMISTORS FOR FIELD USE

The use of electrical resistance temperature indicators ("thermistors") is increasing in many fields of biological investigation. The following is a description of a simple method of mounting rod-type thermistors such as those manufactured by Friez Instrument Division, Bendix Aviation Corporation, Baltimore, Maryland, for field use. This assembly consists only of materials which are easily obtained, and may be constructed with a minimum of tools and equipment.

The main protection for the thermistor consists of a small glass tube of the type that contains individual doses of dental local anesthetic. Usually these may be obtained in some quantities from any dentist. The thermistor is placed inside with the wire leads projecting through the rubber stoppers at each end of the tube. If the thermistor lead wires are first bent into a hook at the tip, they may be pulled through the rubber stopper with a sewing needle. By means of a hypodermic syringe the tube is almost filled with dash-pot oil. A small air-bubble is left in the tube to act as an expansion chamber. The thermistor leads are then soldered to the waterproof outside wire leads which may be connected to any resistance meter. Suitable leads are manufactured by Wood and Metal Products Co., Bloomfield Hills, Michigan. Next, this soldered joint, including the ends of the glass tube and the first inch of the rubber-covered part of the soil lead wire, is coated with sealing wax. After this, the sealing wax, adjoining inch of wire, and a little more of the glass tube are snugly wrapped in plastic self-bonding tape.

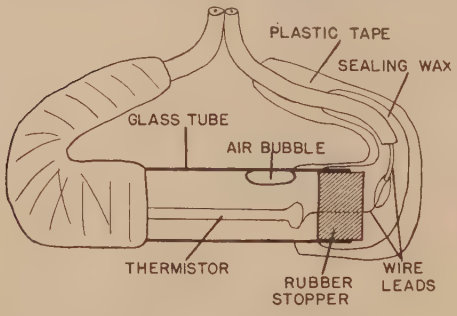

FIG. 1. Details of thermistor assembly. Internal construction at right.

This completed assembly (Fig. 1) allows the glass tube containing the thermistor to be in contact with the soil at its center portion, while the ends and wire contacts are securely sealed against moisture.

Eighteen of these assemblies were used in a fourteen-month field study of physical conditions in small mammal habitats in northern Lower Michigan. They were buried at 1, 3, and 6 inches in Rubicon sand, Emmet sandy loam, and Carbondale muck, and exposed to the soil climate through two summers and a winter, at temperatures ranging from 25 to 101° F., and to soil moisture ranging from 0 to 87 percent by weight. At the end of this period they were returned to the manufacturer for re-calibration and inspection. The results of this calibration were ". . . that the thermistors are in excellent condition and could be used satisfactorily for further work." This method of sealing the assemblies was judged successful ". . . insofar as preventing the entrance of moisture which would tend to destroy their operating characteristics." (E. R. Harrall, Manager, Industrial Sales, *in. litt.* 25 October 1951.)

Undoubtedly, other neater and more efficient assemblies are possible for a thermistor of this shape, but this assembly is cheap, easily constructed, and serviceable. It is ideally suited for a semi-permanent installation in soil or bioclimatic investigations.

WILLIAM O. PRUITT, JR.
MUSEUM OF ZOOLOGY,
UNIVERSITY OF MICHIGAN,
ANN ARBOR, MICHIGAN

OUTLINE FOR ECOLOGICAL LIFE HISTORY STUDIES OF VASCULAR EPIPHYTIC PLANTS

INTRODUCTION

Several of the earlier papers in this series of autecology outlines (Pelton 1951; Penfound 1952; Stevens and Rock 1952) have included extensive treatments of general methods, and have presented detailed outlines of the life histories of specific plants or plant types which of necessity covered many phases common to all plants. These papers, together with the earlier treatments of Ganong (1907), Lawrence (1950), and Richards, Clapham, and Pearsall (1947), are adequate sources of general life history information. Accordingly, the present paper, in dealing with vascular epiphytic phanerophytes,

will place most emphasis on those study methods and life history details which are peculiar to the epiphytes or are accentuated by the epiphytic life form. No provision is made in the outline for taxonomic or systematic studies, for exact descriptions of the species under consideration, nor for a geographical, climatological or geological account of the region of investigation. It is assumed that such information would be provided in any life history study and that epiphytes do not differ materially from other plant types in these particulars. An attempt will be made to cite in the outline those papers which illustrate the particular items concerned.

No generally accepted scheme for the classification of the various types of epiphytes has thus far been proposed. Schimper (1888) offered a four-fold division: *Proto-epiphytes,* which obtain water and mineral nutrients from the supporting substrate or from the air; *Hemi-epiphytes,* which begin their life upon the supporting host but subsequently extend roots to the ground and may eventually become independent of the host even for support; *Nest-epiphytes,* which cause the active collection of humus and water between themselves and their hosts by special growths of the roots, leaves or other structures; and *Tank-epiphytes,* which collect water and mineral nutrients in special tanks or cisterns formed by the leaves and which are rootless or use their roots only for anchorage. Pessin (1925) suggested a three-fold classification: *Eu-epiphytes,* which obtain water and mineral nutrients directly from the air; *Hemi-epiphytes,* which obtain these materials from the substrate, and *Pseudo-epiphytes,* which are ordinary terrestrial plants which occasionally germinate and grow for a time as epiphytes but which are unable to mature and reproduce there. Oliver (1930) rejected these two systems and proposed one of his own based on water requirements. His major groups were: *Hydrophytic epiphytes,* with no special means of protection against water loss by transpiration; *Mesophytic epiphytes,* with aerial parts protected by a cuticle but with no special adaptation for absorbing or storing water; and *Xerophytic epiphytes,* with special devices for absorption and storage of water, as well as protection against excessive loss.

Pittendrigh (1948) has subdivided Schimper's proto-epiphytes and tank-epiphytes into 9 separate types to encompass the variation found in the epiphytic Bromeliads of Trinidad while Simmonds (1950) similarly expanded the hemi-epiphyte division to include those climbing Aroids of the same island which begin their life on the ground, ascend the trees as lianas, and eventually lose stem contact through decay but retain root contact with the soil. The recent studies, especially those of Pittendrigh, indicate that all degrees of intergradation exist between the various "types" of epiphytes and support the view that here, as in other branches of ecology, little is to be gained by the erection of pigeonhole classification systems which are highly artificial.

For purposes of this outline, an epiphyte will be taken to be any nonaquatic pteridophyte or spermatophyte that commonly or regularly grows upon and is supported by another member of these groups, but which is not parasitic upon the supporting plant, and which does not have a stem connection with the ground at maturity. In actual practice, the greatest share of available information deals with true ferns and angiospermous herbs or shrubs growing upon trees in tropical or subtropical regions.

As in the case of other phanerophytes (Pelton 1951), those species of epiphytes which are of economic importance have been most thoroughly studied. This is particularly true of the *Orchidaceae,* whose tropical epiphytic members have received a tremendous amount of attention, due to their great horticultural interest and consequent high monetary value. The great bulk of the references to be cited here refer to the orchids, and to this extent the bibliography is highly unbalanced.

General Treatments of Epiphytes

There have been relatively few recent accounts of epiphytes as a whole or of the epiphytes of a particular region from an ecological viewpoint. Most of the general information available is to be found in the works of Schimper (1884, 1888, 1903) and in the encyclopedic accounts in Handworterbuch der Naturwissenschaften (Karsten 1913) and similar treatises. A recent popular treatment is that of Naylor (1945). Detailed local studies in Java (Van Oye 1924; Went 1940), New Zealand (Oliver 1930), and Trinidad (Pittendrigh 1948; Simmonds 1950) contain much information of general interest.

Epiphytic species are found in many plant families, with greatest representation in the *Filicinae, Araceae, Orchidaceae, Asclepiadaceae, Rubiaceae, Melastomaceae, Cactaceae, Ericaceae, Clusiaceae* and *Gesneriaceae.* The appropriate volumes of Engler and Prantl's Die Natürlichen Pflanzenfamilien contain much material of value on the epiphytes of these groups. A relatively complete account of the life history of *Tillandsia usneoides* has been given by Billings (1904) and Penfound and Deiler (1947). No other similar investigation of a single species was noted.

In the following outline, references to methods are included with the appropriate item affected by the method.

SUGGESTED OUTLINE

Development of the individual plant

Development from fertilized egg to mature plant, with emphasis on critical points in the life cycle and on special morphological adaptation related to the epiphytic habit.

Embryology.—Number of ovules per ovary; number normally developing into embryos; morphology of ovules (Gow 1913; Lindschau 1933; Swamy 1943); prevalence of apogamy (Duthie 1915); number of embryos maturing to seeds (Duncan and Curtis 1943); morphology of embryos (Netolitzky 1926; Swamy 1947, 1949); specialized nutrition of embryo, as by haustoria (Swamy 1948); location and kind of stored food in the seed (Knudson 1922; Burgeff 1936); dry weight and size of seeds (Burgeff 1936); average number of seeds per fruit (Karsten 1913; Burgeff 1936).

Seed dispersal.—Mechanism of fruit opening (Prillieux 1857; Horowitz 1901); special means for releasing seeds, as elaters, etc. (Beer 1857); method of seed dispersal, as wind, birds, insects, gravity, etc. (Karsten 1913; Oliver 1930; Ridley 1930; Curtis 1933; Penfound and Deiler 1947; Simmonds 1950); season of seed dispersal and climatic conditions at that time; distance seeds may be dispersed; seed longevity (Jancke 1915; Wolff 1924; Kundson 1940); environmental conditions favoring seed longevity.

Seed germination.—Season of germination (Billings 1904); environmental conditions at that season (Penfound and Deiler 1947); special conditions necessary for germination (Heinricher 1902; Bernard 1909; Knudson 1922; Mercier 1926; Burgeff 1936); relation of germination to mycorrhizal fungi (Bernard 1909; Burgeff 1936; Curtis 1939); percentage germination under specified conditions (Burgeff 1936).

Seedlings.—Gross morphology of seedlings (Bernard 1909; Burgeff 1936; Penfound and Deiler 1947); growth habit of seedlings, as monopodial or sympodial; origin and longevity of first roots (Billings 1904; Bernard 1909); relative survival percentage of seedlings under specified environmental conditions; nature of optimum substrate, as tree bark, moss layer, soil pockets, etc. (Curtis 1946; Simmonds 1950); time interval from germination to maturity (Knudson 1930).

Roots.—Aerial roots, their gross morphology (Lierau 1888; Palla 1889; Curtis 1917; Bloch 1935); their origin (Unger 1854; Heim 1946); their length (Curtis 1946); their growth rate under optimum conditions, and their longevity; special structures for water intake, as the velamen layer (Meinike 1894; Nabokish 1899; Pirwitz 1931; Engard 1944); mycorrhizal roots (Bernard 1909); photosynthetic roots as in *Taeniophyllum, Phalaenopsis,* etc. (Wiesner 1897; Muller 1900; Doctors van Leeuwen 1920); negative geotropism, as in *Grammatophyllum, Anthurium,* etc. (Linsbauer 1907; Czapek 1909; Cooper 1935); relation of negative geotropism to the nest-epiphyte habit; presence or absence of two kinds of roots (anchoring vs. absorbing—Schimper 1888; Went 1895; Porsch 1911); special root development in leaf tanks or cisterns (Thiselton-Dyer 1902; Pittendrigh 1948).

Stems.—Special adaptations for water storage, as in pseudobulbs, etc. (Pfitzer 1882, 1884; Hering 1900; Curtis, K. M. 1917; Curtis, C. H. 1943); epidermal coverings to reduce transpiration (Mez 1904); branching habit (Lindinger 1910); location of dormant buds; longevity of dormant buds; adventitious buds, (Raciborski 1898).

Leaves.—General morphology of leaves (Pfitzer 1882; Dalitzch 1886; Mobius 1887; Hoffman 1930; Oliver 1930; Keiline 1915); internal water storage and tissues involved (Oliver 1930; Cooper 1938); adaptations of leaves for water collection, as individual cistern leaves in Asclepiads (Thiselton-Dyer 1902); or tanks made of several leaf bases, as in Bromeliads (Schimper 1888; Pittendrigh 1948), or epidermal outgrowths and scales for direct water absorption (Mez 1904; Tietze 1906; Pessin 1924; Potts and Penfound 1948); adaptations of leaves for collection of organic detritus, usually accompanied by a leaf dimorphism, as in the thalloid pocket leaves of *Platycerium* (Schimper 1888; Goebel 1889); other leaf adaptations, as openings in the leaves of "hurricane" plants (Trecul 1854); or rolling of the leaves, as in Bromeliads (Ziegenspeck 1935; Potts and Penfound 1948).

Flowers and fruits.—General morphology of flowers (Hildebrand 1883; Pfitzer 1886; Swamy 1948); sexual dimorphism in flowers (Darwin 1862; Rolfe 1890; Guttenberg 1915; Hawkes 1947); general morphology of fruits (Prillieux 1857; Horowitz 1901); developmental pattern of fruits in relation to internal embryological developments (Duncan and Curtis 1942, 1943).

Physiology of the mature plant

Details of physiological processes which are especially affected by the epiphytic habit.

Nutrition.—Source of mineral nutrients in the aerial habitat, as bark (Dixon 1881); dust from the air (Dixon 1881; Aso 1909; Dubois 1925); or materials in solution in rain water (Truffaut 1893; Lieske 1915; Voth 1939); accumulations of organic detritus between epiphyte and host or in special catchment organs of epiphyte (Oliver 1930; Went 1940; nature of humus in substrate (Pessin 1925; Oliver 1930); concentration of nutrients in root-bathing liquids (Curtis 1946); ionic composition of root-bath-

ing liquids (Curtis 1946); ion uptake as shown by tissue analysis (Truffaut 1893; Moran 1894; Harper 1919; Harris 1926; Tienken 1947).

Water relations.—Osmotic pressure of tissue fluids (Harris 1918); efficiency of aerial roots in water uptake (Kamerling 1911; Wallach 1939; Davis 1946); direct absorption of water from air by roots (Wallach 1939), or by leaves (Mez 1904; Pessin 1924; Potts and Penfound 1948); the tank habit in relation to water supply—amounts collected, persistence of supply, mechanism of absorption from tank, etc. (Schimper 1888; Moewes 1914; Pittendrigh 1948); transpiration rates (Witt 1909; Kamerling 1911; Pessin 1924; Penfound and Deiler 1947; Potts and Penfound 1948).

Flower induction.—Influence of day length; season of appearance of flower initials (Johnson and Laurie 1943; Rotor and MacDaniels 1951); interval between differentiation of initials and anthesis (Johnson and Laurie 1943; Rotor and MacDaniels 1951); thermoperiodic responses; occurrence of gregarious flowering and its correlation with environmental changes (Went 1915; Seifritz 1923; Coster 1926; Smith 1926; Kuijper 1933).

Flower biology.—Annual fluctuation in numbers of flowers per plant; season and duration of anthesis (Kranzlin 1910; Warne 1934); correlation with wet and dry seasons or other environmental fluctuations; usual pollinating agents (Moewes 1913; Porsch 1926; Carr 1928); adaptations to aid pollination (Darwin 1879; Ames 1941); nectar secretion (Coleman 1938); changes accompanying pollination (Hsiang 1951; pollen longevity (Curtis and Duncan 1947); self-sterility (Scott 1865); autogamy (Forbes 1886, Smith 1929); respiration rates of flowers, especially those with internal temperatures higher than surrounding air (Kraus 1896; Leich 1915); reproductive efficiency in terms of number of flowers per fruit, number of fruits per plant.

Vegetative reproduction.—Usual methods of vegetative reproduction (Lindinger 1910; Doctors van Leeuwen 1920); relative efficiency of vegetative vs. sexual methods (Penfound and Deiler 1947); environmental conditions conducive to vegetative reproduction; longevity of mature plants (Pring 1944; Cooper 1946).

Environmental relations of the mature plant

General and specific studies of the effects of single or multiple factors of the environment, especially microclimatic correlation studies aimed at explaining observed local occurrences of epiphytes.

Light.—Average light intensity for optimum growth (Bungeroth 1891; Lefebre 1894; Wiesner 1895; Schlecter 1912; Oppenheim 1917; Pessin 1925); shade tolerance (Schimper 1888; Van Oye 1921; Oliver 1940; Pittendrigh 1948); special conditions under which normal sun-epiphytes may grow in shade (Shreve 1911; Oliver 1930; Pittendrigh 1948); measured compensation points; effect of daylength on growth (Ratzek 1932).

Temperature.—Average, daily range, and seasonal range of temperatures for optimum growth (Gilbert 1934; Warne 1938; Went 1940; Dunn 1941); relation between light, temperature, and humidity (Lefebre 1894; Oppenheim 1917; Dunn 1941; Pittendrigh 1948); frost hardiness of species (Dusen 1918); special effects of temperature on flowering.

Atmospheric humidity and precipitation.—Daily and seasonal range in humidity in locations of optimum growth (Raciborski 1898; Warne 1938; Penfound and Deiler 1947); variation in humidity at various vertical levels on host tree (Pessin 1925; Pittendrigh 1948); special moisture conditions in cloud forest (Curtis 1947); relation of humidity to wind at various vertical levels (Oliver 1930); seasonal distribution of precipitation (Went 1940; Pittendrigh 1948); extent and severity of dry season.

Synecology

Epiphytic communities, their relation to forest communities, succession, host specificity and other biotic relations. The study of epiphytic communities presents many methodological difficulties, particularly with regard to sampling procedures. The possibility of a definite host specificity greatly complicates any attempt at random sampling, while the physical difficulties of observing and measuring the epiphytic flora on 100–200 feet tall rain-forest trees offer truly formidable obstacles (Black, Dobzhansky, and Pavan 1950). As a result, detailed synecological studies comparable to those usual on temperate zone herbaceous plants are very rare. The only one with any pretention of completeness is that of F. W. Went at Tjibodas, Java (1940), although excellent partial studies were made by Oliver (1930) and Pittendrigh (1948). Papers which illustrate the various synecological methods that are used in epiphyte studies are those of Went (1940), Ochsner (1928), and Pittendrigh (1948). Went gives details as to his use of binoculars for determination of the epiphyte flora of rain-forest trees.

Epiphytic communities.—Regional groups of species which commonly grow together (Schimper 1888; Gallemaerts 1911; Oliver 1930; Went 1931, 1940; Eggeling 1947; Pittendrigh 1948; Simmonds 1950); distribution of epiphytes in relation to favorable host plant communities

(Oliver 1930; Went 1940; Eggeling 1947; Pittendrigh 1948).

Succession.—Age of host branches at time of establishment (Went 1940; Simmonds 1950); preceding and following epiphytes (Van Oye 1924; Oliver 1930); general trend of succession in relation to changes in habitat factors, as depth of detritus, increasing shade, or changed moisture relations (Dudgeon 1923; Oliver 1930); nature of "climax" community; causes of catastrophe, as wind, increasing weight of epiphyte mass, shedding of bark on host tree, etc. (Oliver 1930).

Host specificity.—Observed host range of epiphytic species (Bungeroth 1891; Schimper 1888; Oliver 1930; Pittendrigh 1948; Sulit 1950); relative abundance on different hosts (Pessin 1925; Went 1940); host characteristics favorable or unfavorable to epiphytes (Goebel 1889; Oliver 1930; Penfound and Mackaness 1940; Pittendrigh 1948); water-retaining capacity of bark (Pessin 1925; Dravin 1940; Went 1940); general environmental characteristics of favorable host plant communities (Allee 1926; Oliver 1930; Went 1940; Pittendrigh 1948); detrimental effects of epiphyte on host, as in killing branches, etc. (Cook 1926).

Biotic relations.—In addition to the usual interrelations with other organisms, such as fungus diseases, animal enemies, dispersion by animals and the like, many epiphytes show peculiar and intimate symbiotic interactions with certain animals that make their homes within the epiphyte. These specialized instances have been studied in fair detail in both New and Old World tropics and should be looked for in any epiphyte study.

Ant nests.—Leaf or stem modifications to provide internal cavities suitable for ant nests, as in *Myrmecodia* and *Hydnophytum* (Treub 1883, 1888; Miehe 1911); presence of Belt's corpuscles or Muller's corpuscles (Schimper 1903); species of ants using the nests (Doctors van Leeuwen 1929, 1933); season of year ants are present; relation of ants to accumulation of detritus (Ule 1904); Wheeler 1921; Weber 1943); other insects or fungi associated with ants (Weber 1943).

Aquatic animals in tank epiphytes.—Animal species breeding in tanks, including invertebrates and vertebrates (Scott 1912; Picado 1913; Dubois 1925; Dunn 1937; Neill 1951); seasonal relations to faunal population; relation to malarial vectors and other disease carriers (Roseboom and Laird 1942; Downs and Pittendrigh 1946; Pittendrigh 1948); possible control measures for such disease organisms.

Insectivorous species.—Method of trapping insects; species utilized; seasonal relations.

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John T. Curtis
Department of Botany,
University of Wisconsin,
Madison, Wisconsin

OUTLINE FOR ECOLOGICAL LIFE HISTORIES OF SOLITARY AND SEMI-SOCIAL BEES

The bees belong to the superfamily Apoidea of the insect order Hymenoptera. According to the most recent catalogue (Muesebeck, Krombein, and Townes 1951) the portion of North America lying above the Mexican boundary contains 6 families, 99 genera and 3,287 de-

scribed species and subspecies of bees. Of these, 119 species and subspecies are social in habit (including parasitic forms [1] derived from social types), the remainder are solitary or semi-social (including parasitic forms derived from solitary and semi-social types). Since the ecological problems associated with the study of social bees are in many cases different from those involved in the study of solitary and semi-social bees, it is proposed to limit the scope of this outline to the latter groups.

Solitary bees may be defined as those species in which each female constructs her own nest consisting of one or more cells and in which the larval food supply is sealed after an egg has been deposited. If these nests are regularly placed in groups in close proximity to one another the species is described as gregarious. Semi-social bees also construct individual nests with sealed cells but they usually share a common entrance and sometimes have a partial division of labor. The true social bees (excepting the parasitic forms derived from them) share construction of the nest and most other activities, have a distinct division of labor involving a worker caste consisting of essentially nonreproductive females, live in colonies in which a single queen carries on the reproductive activities for the group, and the larvae are fed progressively, except in the Meliponini.

Of the 3,166 North American species of solitary and semi-social bees, reasonably complete ecological life histories are known for less than a dozen. However, something of the nesting habits is known for about half of the non-parasitic genera (Malyshev 1920, Nielsen 1934, Michener 1944). From these studies it appears that most species nest in the soil. However, such genera as *Hylaeus, Megachile* (many species), *Clisodon, Ceratina,* and *Xylocopa* nest in pithy stems, twigs, or wood. Most megachilids utilize pre-existing cavities for nest sites; *Xylocopa* usually excavates its burrows in solid wood.

Individual cells may be constructed of soil (most ground nesting species) or lined with a papery secretion (as in *Colletes* and relatives), waxy materials (*Andrena, Anthophora,* and others), leaves or petals (*Megachile*), chewed-up leaves (*Osmia*), or plant down (*Anthidium*); or they may be constructed of resin, pebbles and sand (*Dianthidium*). The cells may be placed end to end in a regular series (as, for instance, *Colletes, Megachile, Anthophora, Xylocopa*), in alternate series (*Andrena, Halictus*), in clusters (*Nomia,* some *Dianthidium*), or singly (*Anthidiellum*).

The pollen provisions of the cells also vary characteristically. In some cases (*Colletes, Megachile, Anthophora*) the pollen is moistened with nectar or water and either packed into the bottom of the cell or stored dry with liquid on the top. In other instances (*Andrena, Halictus*) it is packed in a ball-like mass. The position of the egg, in relation to the pollen mass also varies and is an important biological character.

Since all of the non-parasitic solitary and semi-social bees collect pollen as food for the larvae, they obviously play an important role in the pollination of many plants (Müller 1883, Loew 1884, Knuth 1906–09, Grant 1950, etc.). Thus, pollen constancy is useful in evaluating the effectiveness of both species and individuals of pollinating bees. Loew (1884) applied the term heterotrophy to the differences which he observed in flower-visiting habits of bees with tongues of about equal length. On this basis he recognized three types, monotropic, oligotropic and polytropic bees, depending upon whether they visited a single species of plant, related species of plants, or unrelated species of plants, respectively. Since these terms were applied to nectar as well as pollen visits, Robertson (1925) proposed the terms monolectic, oligolectic, and polylectic for the pollen visits of bees.

Special Methods and Techniques

It is obvious that with the large number of bees now known, ecological relationships will be extremely varied. Thus the following methods and outline for study, although suggestive, cannot be expected to fit in their entirety the needs of an ecological life history study of any one species. Many of the methods and techniques outlined here have been developed for the honey bee but are applicable to studies of solitary and semi-social bees.

Sampling populations. Various sampling methods will reveal diurnal and seasonal activity trends of many kinds as well as information on sex ratio, competition, host preferences, flight range, parasitism, and the effects of weather. The purpose of the sampling should be kept in mind when selecting the appropriate technique.

The use of direct counts of adult bees is one of the oldest methods of developing quantitative data on bee populations. Counts to determine trends from day to day or week to week should always be made at the same time of day and variations in weather conditions should be taken into account. It is a common practice to make two counts each day—one in the morning and one in the afternoon. The direct counts may be made for certain time intervals (Brittain 1933, Morrison 1943), areas, or numbers of sweeps of a standard net. Various workers (Knowles 1943, Peck and Bolton 1946, and others) have used areas of several sizes and shapes, but the most widely used is the USDA

[1] This term is here used broadly for those species which do not collect pollen but which live at the expense of pollen-collecting forms.

method (Vansell and Todd 1946) where the bees are counted in ten square-yard areas and the total multiplied by 484 to give an estimate of the number of bees per acre. The sweep method and the USDA method are especially applicable where blossoms are uniformly distributed over large areas (as in commercial plantings). The USDA method currently being used in Utah involves the use of previously laid out string lines demarking square-yard areas for more precise counting (G. E. Bohart, *in litt.*).

The sweeping method, although more tedious, has certain advantages over the area method. With proper precautions as to uniform sweeping, the variations between individual counters is minimized and there is more chance of recording those species which are very rapid in their movements or easily disturbed. However, neither method provides samples of the more elusive types in the same proportion as the slower forms. In order to avoid disturbance of the elusive species, or to make observations of bees in inaccessible places, binoculars have been used (Vansell 1942).

For many purposes the sweeping method has a further advantage over area-sampling in that specimens may be preserved for laboratory examination. In general practice, a standard number of sweeps is made in a uniform manner, and the bees, still in the net, are placed in a large cyanide jar. When the bees are dead they may be counted and examined with ease (Linsley 1946). Linsley and MacSwain (1952), who attempted to follow trends in a small population of *Andrena complexa* Viereck, swept up the entire flower-visiting population each day and transferred it to a darkened gallon jar. The bees were allowed to escape one at a time through a glass tube (six inches long and with a diameter slightly larger than the bee). This technique was harmless to the individual bees, did not markedly disturb the population, and permitted a very accurate check on sex, parasitism, identifying marks, etc., of each individual. However, in the case of some parasites, acurate data can only be obtained by a dissection of the host.

The sweeping net used in most ecological work has had either a twelve- or a fifteenth-inch hoop (Phillips 1931), but there has been little standardization in other features of the net or sweeping methods. Smith and Smith (1951) have proposed a standard 15-inch sweeping net. We have used this net with a larger mesh bag for bee work. A standard net would permit more direct comparison of samples taken by workers studying the same problem in different areas.

Short-term oscillations due to weather conditions and other factors may be eliminated from trend curves by the use of moving averages (Kendall 1941).

When nests are concentrated it may be possible to use the method of Bohart and Liebermann (1949) who delimited areas in the nesting site and then counted the open nests in the early morning. As the counts were made each nest was pinched shut without destroying the bees' landmarks; thus each count represented the active nests of the period since the prior count. This method requires that the soil surface be moistened if it is not already sufficiently damp to permit pinching.

Periodic samples of nests from several nesting sites helps to establish the seasonal occurrence of various developmental stages and to provide a check on laboratory rearing data. These samples also provide information on parasitism.

Emergence screens, *i.e.*, fine-mesh screen fastened tightly to the ground over the nesting area, may be used to ascertain seasonal and diurnal cycles of emergence of the sexes, parasites, predators and inquilines (Linsley *et al.* 1952). They are especially valuable for those species which are short-lived as active adults. Screens which have a door for removal of the insects are easiest to use. These screens may also be used to cover a portion of the nesting site and thus exclude nesting activity during a particular portion of the year. Excavation at the end of the active season will give a comparison of activity in different portions of the year.

Pollen load analysis. Qualitative and quantitative analysis of the pollen on various parts of the bees' bodies and throughout the season has proved a valuable tool in studies of the honey bee and deserves wider use in studies of wild bees (Betts 1920, Clements and Long 1923, Brittain 1933, Brittain and Newton 1933, Hare and Vansell 1946, Percival 1947, Grant 1950, and others). Custer (1928) and Linsley and MacSwain (1942) combined observations of the pollen-collecting habits of the bees with an analysis of the stored pollen in the cells. For proper interpretation pollen analysis and identification should be made to the specific level and should be correlated with the abundance and sequence of blooms in the area. Wodehouse (1935) and Erdtman (1943) are excellent references to the general subject of pollen analysis. The number of loads per cell can be determined by direct observations of the bees, by differences in consistency or colors of various loads, or by comparing the weight of a single load with the weight of the total provision.

Marking. A wide range of materials has been used to mark bees and other insects for studies of flight range, longevity, and for other purposes. The methods used roughly fall into two categories—individual marking and mass marking.

Individual marking is usually accomplished by

placing small spots of various colored quick-drying paints on the thorax and other parts of the body (Fabre 1879–1907, Müller 1882a, Custer 1928, Park 1929, Minderhoud 1931, Eckert 1933). Park (1929) reports white, pink, yellow, orange, red, light green, and blue to be readily distinguishable on bees and gives a simple system for marking 63 individuals differently. Von Frisch (1923, 1950) describes a system which permits the marking of 599 individuals. Linsley and MacSwain (1952) found clipping the tip of one or the other or both wings more permanent than marking and combined it with the use of dyes and aluminum dusts.

Mass marking has proven more difficult than individual marking. Numerous materials, of varying permanence and suitability, have been used to mass-mark various insects. Among them are chalk (Copeman *et al.* 1911), aniline dyes (Zetek 1913, Parker 1915, and others), bronzing powders (Russell and Rao 1942) and fluorescein (Musgrave 1949, 1950). Care should be taken in mass marking that the bees are not injured either through gumming of their wings, eyes, or mouthparts, or through toxic action. Smith *et al.* (1948) mass-marked an estimated 7 to 10 percent of the field force of a number of colonies of honey bees with a spray of basic fuchsin, and 1600 individuals with a spray containing titanium dioxide. The use of radioactive materials has proven of value in the investigation of mosquito flight range (Hassett and Jenkins 1949, Jenkins 1950, Thurman and Husbands 1951, Yates *et al.* 1951) and movements of soil insects (Fuller *et al.* 1951). It also may have a place in bee studies.

Special rearing methods. Because bees spend a large part of the year in cells and burrows it is necessary to resort to special rearing techniques to determine their detailed life histories and the factors influencing them. Although laboratory studies reveal facts not observable under field conditions, it must be kept in mind that the organisms may not be reacting normally under such conditions. Immature bees of many species are very susceptible to attack by molds and to desiccation in atmospheres of low humidity. Others, such as the megachilids, are more resistant and require less care in rearing. Group rearing may be conducted in Petri dishes containing moistened sterile sand. Linsley *et al.* (1952) have described a wax-coated rearing dish for individual bees.

Numerous types of small rearing cages are available (Peterson 1947) and some have been used for bees (Eckert 1945, Way and Synge 1948, Woodrow 1948, Linsley *et al.* 1950, and others). When these cages are held at high humidities and temperature below 30° C. the cage survival of most of the species of wild bees is satisfactory for periods of 24 hours (Linsley and MacSwain 1947a, Linsley *et al.* 1950). Bohart (*in litt.*) reports that clipping the wings increases the survival period in cages. Clements and Long (1923), Knowles (1943), Carlson (1946, 1950), McGregor and Vorhies (1947), and others have used field cages for various purposes.

Enticing bees to artificial nests. For observations on their habits and biology, bees may be enticed to specially-prepared easily-available nesting sites and into artificial nests (Nicholas 1890, Friese 1923, Malyshev 1924, 1932, Hardouin 1948). Malyshev (1925, 1928) enticed *Anthophora acervorum* to specially constructed clay blocks. He also demonstrated the source of materials used in building cells and the disposal of excess materials by observing nest building in a box filled with different-colored layers of earth. Friese (1926) dscribes an artificial clay bank into which colonies are introduced. He also describes the use of hollow stalks and glass tubing to attract bees for observation. Hartmann (1943, 1944) used glass tubes as artificial burrows and made photographs of bee activities in the nest. These artificial burrows may be varied in size and shape to determine the requirements of the bee and their effects on development (Rau 1937). The volume of the cells may be determined by measuring the amount of sand, plaster of Paris, or wax required to fill them (Malyshev 1936). Holes for nests may be drilled in posts, logs, and banks.

All-day observations. Observations of the activity in a restricted section of the nesting area offer information on nesting behavior of female bees, duration and rate of pollen trips under various conditions, time required to provision a nest, rate of burrow construction, mating, activity of parasites, etc. These observations are most valuable when made at intervals during the nesting season and throughout the daily period of adult activity. The area selected should be staked and mapped and the nests numbered and marked. In soft ground, small numbered or colored pot stakes are useful; in harder ground, colored thumb tacks or sharp wire stakes will be more satisfactory. It usually requires at least two people to make observations on nest-site activities (one observing and one recording with a watch). All-day observations in the nesting site can be best interpreted when coupled with complete excavations of the marked nests at the end of the season.

All-day observations should also be made of the bee activities in relation to flowers. The time and number of flower visits required to complete a pollen load, flower constancy, times required for various kinds of visits, and diurnal cycles of activity are especially important. The stop watch and hand tally are valuable tools for this work (Linsley 1946, Vansell and Todd 1946). It is important to distinguish

flowers which are visited merely for nectar and the flowers which serve as a source of pollen. It is usually necessary to determine the life history, development, and floral structure of the principal pollen plants. Systematic observation of marked flowers and buds is usually a satisfactory method for this purpose (Knowles 1943, Linsley *et al.* 1952). A very useful chart for recording this type of behavior has been used by Linsdale (1946).

Experimental pollination and behavior studies. The flower-visiting habits of bees have been the well-known objects of behavior studies by Plateau, Bonnier, Forel and many others. For reviews of methods and techniques in these studies see Knoll (1921–26), Porsch (1922), and Clements and Long (1923). The recent summary by Frisch (1950) of his work with the honey bee is a model of scientific investigations in bee behavior and some of his approaches and techniques might well be adapted to problems of solitary and semi-social bees.

Locating of bee nests. Adequate information relative to the ecology of any bee species cannot be obtained from a single nest. Information such as the seasonal distribution of the growth stages, variation in nesting activities, sex ratios, or percent of occurrence of parasites or predators or inquilines, and many other kinds of data can only be secured when adequate cell series are available. Different bee genera and species construct their nests from a wide variety of materials and in almost all terrestrial habitats. Although no detailed discussion can be undertaken here, a few generalizations may prove of value.

During the active season of the adult bee, nests may be found by hunting in areas where many individuals of the species are associated with their pollen and nectar sources. In such an area observation of the flight direction of pollen-laden females or of unladen females coming to the flowers may lead to the nesting site. However, in some instances the bees will be found nesting in the soil between the flowering plants. The mating-flight behavior of male bees may also reveal nesting areas even when no nests are apparent or before females have emerged. In addition, following female bees of parasitic species will often lead to hidden nests. The parasites not only indicate the general ecological niche of the host species, but, by returning to burrows which they have previously visited, will reveal individual nests. In addition nests of many species may be located by watching for activity around sandy or clay banks, barren areas of soil in areas of dense vegetation, beetle-riddled logs, hollow twigs, sandy areas and many similar habitats favored by different genera and species of bees. Finally, bee nests may frequently be found, even on days when the adults are not flying, by searching in suitable areas for various evidences of bee activity. Such evidence as open holes in the ground or banks, protective chimney-like turrets, and piles of freshly excavated earth will allow the investigator to locate nests during periods of bee inactivity due to inclement weather. In general, the openings of bee burrows may be distinguished from those of ants, beetles, earthworms, spiders and other miscellaneous soil-inhabiting animals by their circular shape, uniform size and unbeveled lip. Furthermore, the entrance shaft is circular and uniform in diameter and the walls are smooth.

In the inactive season the problem of searching for nests is somewhat more difficult. Some species which attach their nests to twigs, branches or rocks may be more readily found than in the active season. Species which utilize cliffs or well-drained ground or logs may be recognized by unweathered turrets, or characteristic plugs of mud or chewed vegetation or pitch or plant down, or by the characteristic size, shape, and age of an unplugged burrow. Cells constructed in the cavities of old mud nests of other bees or wasps or in hollow twigs may be profitably gathered at this time and held for future emergence. Nests in flat sand or broken ground are most difficult to locate shortly after the close of the active season and in general can be excavated only with a prior knowledege of their exact location.

Excavation. The excavation of burrows of ground-nesting bees is a tedious and difficult task. Malyshev (1933) gives details on the preliminary examination of the nest from the entrance, investigation with a catheter, preliminary excavation, preparation of the tumulus, filling the burrow with plaster of Paris or molten metal, collecting the bee, extracting the nest, finding the cells, and opening the cells. In our experience proper preparation of the site is essential. It is usually most convenient to dig a hole beside the nesting area considerably deeper than the length of the burrows. The burrows are then exposed by cutting toward them slowly and carefully. A small straw placed in the burrow helps to determine the direction of the burrow and will help to avoid losing the nest when soil falls into the burrow. Trapping the bee in its burrow may serve much the same purpose.

Various materials have been introduced into the nest to facilitate its excavation. The most widely used is plaster of Paris (Smith 1898a, 1898b, 1901, Malyshev 1926, 1927a, 1927b, 1928, 1930, 1933, Christensen 1931, Nielsen 1931, 1934). The nest is opened by carefully removing any debris closing the opening. First a mixture of one part high quality plaster to three or five parts water is introduced into the nest. Then the nest is filled with a 1:1 mixture. The plaster mixture is stirred with a straw to make

sure the nest is full. The cast is ready to excavate 20 minutes after the plaster is hard at the opening. In excavating, make a sketch of the angle of the burrow with the surface. The casts are very fragile. Christensen (1931) coated the casts with metal. Nielsen (1931) and Malyshev (1933) used alloys with low melting points (70–80° C.) to mark the burrow and Adlerz (1913) hardened the area surrounding the nest with water glass. All of these methods are of little use when the nests are very complicated or have closed laterals. Nielsen (1931) describes a method by which wax models can be prepared of such complicated burrows by successive plotting of thin layers. Such equipment as a shovel, mattock, geologist's pick, small pry-bar, trowel, brushes, knives, bellows, steel tape, calipers, forceps, vials, hand lens, camera, and pill boxes will be found useful. Adlerz (1903) used a small mirror to reflect light into the excavation.

General records. Daily precipitation and temperature records from a near-by weather station may be of value for some purposes, but since radiation is especially important to poikilothermic animals living near the surface of the ground, it will be necessary to supplement such data with other records. Consequently, such measures of radiation as the black-globe thermometer (Bedford and Warner 1934) and the Livingston black-globe atmometer are recommended. Shielded air temperatures, relative humidity, air movements, and soil temperatures at appropriate depths will be of value.

A running account in a field notebook is valuable but we have found data recorded on 5×8 inch filing cards most usable. These can be readily shuffled when tabulating data. Rearing records, burrow diagrams, flight records, etc., are kept on separate cards. If necessary, a table or outline can be printed or Mimeographed on the cards to facilitate recording of essential data. Habitat photographs and other photographic records are especially useful.

Parasites, predators, and inquilines. The numerous species of animals associated intimately with bees play an important role in their ecology. These belong to so many diverse groups that no attempt has been made to discuss the special methods and techniques suited to their study. However, many of the items in the suggested outline for the study of the ecological life histories of bees may be applied to parasites, predators, and inquilines with but slight modification.

Suggested Outline

I. General Considerations.
- A. Taxonomy and nomenclature: authoritative identification; description of species including developmental stages; valid scientific name; common names; provision for permanent preservation of specimens involved in the study.
- B. Importance: ecologic and economic.
- C. Distribution: geographic, ecologic, and seasonal; general climatic characteristics of range; effect of barriers; population continuity and density.

II. Description of Habitat.
- A. General locality: exposure, topography, flora, fauna, and climate.
- B. Characteristics of nesting site: soil (drainage, texture, type, salinity, profile, available water and field capacity, pH); temperature (black-globe, shielded-air, and soil at various levels); air movement; sun and shade; distribution and abundance of sites; exposure and slope; associated flora and fauna and microdistribution of bee.

III. Life History of Bee.
- A. Overwintering and emergence: when, where, how; overwintering stage (larvae, unemerged adults, fertilized females); factors influencing emergence (atmosphere, gravity, exposure, vegetation); correlation of emergence with blooming period of pollen flowers; meconium; methods and hazards of egress; cycle of emergence of males and females (earliest, maxima, latest); sex ratio and distribution of sexes in nesting site; diurnal cycle of emergence.
- B. Pre-nesting activity: duration of pre-nesting period, relation to mating, resting sites (diurnal, nocturnal, and seasonal, and location); importance of food and water; ovogenesis (rate and numbers of eggs, relation to fat body, preoviposition period).
- C. Mating and courtship: when, where, and how; frequency; rivalry and combat between males; male territory; polyandry and polygamy; sexual attraction; seeking and selection of males by females or avoidance of males by females; sexual dimorphism; secondary sexual characters.
- D. Nesting activity. (1) Site selection: relation to other nests (colonial, gregarious, pseudocolonial, composite, or solitary; seasonal variation); effect of substratum on gregariousness; relation to microhabitat (soil, slope, vegetation and other cover); adaptations for concealment and protection from the environment. (2) Preparation of nesting site: disposal of debris and other unwanted material. (3) Competition with other insects. (4) Excavation: methods (use of legs, mandibles, water, etc.); formation and character of tumulus, if present (shape, configuration, size); character of entrance hole (closed, open, half-open, concealed); formation and character of turret, if present; influence of substratum. (5) Nest plan: tumulus, turret, entrance hole; character of burrow (diameter, depth, la-

terals, slope, lining); relationship of cells in nest (separate, connected); direction and type of ramification, if any; arrangement of cells within series (linear, ramifying, corporeal, radial clusters, linear clusters); distribution of sexes in nest (effect of sex size; proterandry). (6) Type of nest construction.[2] (7) Cell construction: shape and proportions (effect of nest cavity; variations); walls (number and type of layers, relation to nest cavity); materials (source, type, and use); lining (silk-like, wax-like); partitions; cap; orientation (erect, inclined upwards, horizontal, inclined downwards, inverted, effect of nest cavity); order of cell construction (consecutive, serial). (8) Provisioning of cell: time of, in relation to cell construction; number of pollen trips required; method of unloading pollen (time, thoroughness, method of handling); composition of pollen mass (uniform or mixed, chemical properties of liquid and pollen); ratio of honey to pollen, amount of free liquid, ratio of provision to size of cell; consistency and shaping of pollen; liquefaction, souring, and other changes of provision after storage. (9) Oviposition: time of laying egg; position of egg in relation to food and walls; attachment of egg; orientation of egg; additional secretions. (10) Closure of cell: materials; permeability; layers; texture; additional barricading. (11) Closure of burrow: temporary and seasonal; materials and source; volume. (12) Number of nests and series by one female. (13) Relative size of first nest in relation to others. (14) Effect of age on nesting activities and sex ratio of offspring. (15) Defense of nest. (16) Methods of collecting and transporting nesting materials and water. (17) Flight patterns over nesting site (seasonal changes, orientation, recognition of nest). (18) Diurnal cycles of nesting activities.

E. Other adult activities: use of food, water and shelter; premating activity; postmating activity; intraspecific reactions; interspecific reactions; length of adult life; "sleeping" habits of males and females; means of communication; tolerance; migration; flight range.

F. Development of immature stages: egg (size, shape, chorion); incubation; hatching; disposal of egg membrane; movement of larva; orientation of larva to feed; reorientation; feeding (duration, habits); disposal of excrement (periods, diagnostic characteristics); number and duration of larval instars (effect of sex); molting; disposal of cast skins; cocoon construction; type of cocoon (complete, incomplete, shape, texture, material); larval resting stage; sound production by larval stages; diapause (complete or partial); prepupa (duration and special powers of resistance); semipupa, pupa; preemergence period of adult.

G. Flower relationships: diurnal and seasonal cycles of populations on flowers; diurnal and seasonal patterns of foraging activity; method of visiting flowers; method of pollen collection; method of carrying pollen (position, loose or compact loads, admixture of nectar); flight ranges for nectar and pollen; constancy to foraging sites and individual plants; total daily flower visits for pollen and nectar, total seasonal flower visits for pollen and nectar; visits per minute; visits per pollen load; pollen loads per cell; effect of physical factors (wind, temperature, clouds, humidity, rainfall) on flower visits; nectar plants and their relative importance; pollen plants and their relative importance; competition for bees between pollen plants and nectar plants; means of attraction; flower development and life history; seasonal adjustments of bee to flower succession; single trip, daily and seasonal flower constancy of individuals and species (monolecty, oligolecty, polylecty).

H. Seasonal distribution of stages.

IV. Special Relationships of Bees to Environment.

A. Parasites, predators, and inquiline associates: general activity pattern and development as recorded for bee; method of gaining access to host; effects of parasite on individual hosts; general predators and disease.

B. Competition with other bees.

C. Secular and seasonal trends of host bee and parasites, parasites and disease.

D. Population cycles in nesting areas due to availability of nest sites, effects of parasites, flower abundance.

[2] For a classification of nest types, see Malyshev (1917, 1936).

Acknowledgments

Dr. G. E. Bohart, Division of Bee Culture, U. S. Department of Agriculture, and Dr. C. D. Michener, Department of Entomology, University of Kansas, kindly read this manuscript and offered many helpful suggestions.

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E. G. Linsley
J. W. MacSwain
Ray F. Smith

Department of Entomology and Parasitology,
University of California,
Berkeley, California

PRACTICAL LIMITATIONS OF THE DIAL GAUGE DENDROMETER

Introduction

For various types of investigations, it is desirable to measure the diameter growth of forest trees at intervals of a week and occasionally for time periods as short as one day. The machinist's dial gauge is a precise instrument which Reineke (1932) used to measure the radial growth of a tree, the adaptation being labeled as a "precision dendrometer." Daubenmire (1945) has made a recent improvement on the dial gauge adaptation which has been used by Brown *et al.* (1947) in a silvicultural experiment on the Harvard Forest.

According to Bruce and Schumacher (1950), a dendrometer is a device which can be used to measure the diameter of a tree at any place on the tree bole. The so-called "precision dendrometer" actually only measures the radial increase at some selected point on the tree bole. Inasmuch as there are an infinite number of radii on the tree bole at any given height above the ground, it is only possible to calculate an estimate of the diameter growth at that particular height above the ground using the dial gauge as adapted. To sample properly the population of radii so as to obtain a reasonable average and an estimate of its error as outlined by Schumacher and Chapman (1948) it would be necessary to take several dial gauge measurements at some particular height above the ground on the tree bole. It is the purpose of this paper to present some data indicating the variable rate of radial growth at any particular height above the ground on the tree bole which reduces the effectiveness of the adapted dial gauge, itself a precise measuring instrument, as a dendrometer.

Methods

A loblolly pine (*Pinus taeda* L.) plantation in the Duke Forest, Durham, North Carolina, averaging 37 feet in height and 6 inches in diameter breast high, and 16 years old, was selected for study purposes in June, 1947. Six trees having about 50 percent of the total tree height in crown, at one end of the plantation, were selected to be measured. These trees were selected solely because they were away from the road and, therefore, there was less chance of someone tampering with the screws or metal tags. Dial gauge measurements were made in the vicinity of breast height on each tree.

Of the infinite number of radii at the selected height above the ground, two were to be selected at random on each tree as a measure of the variation between randomly selected radii. The radius directly opposite each randomly selected radius would then be systematically selected to afford two pairs of systematically selected radii on a tree. Thus, it would be possible to compare random samples against systematic samples of radial growth on the tree bole.

The improved model of the dial gauge dendrometer as described by Daubenmire (1945) was employed as well as his suggestions for preparing the trees and the procedure for taking the measurements. Measurements were made weekly from June 7 to November 1, 1947, by the writer.

Results

Weekly changes in the tree radii varied from a maximum of 0.092 inch to a minimum of −0.060 inch. The negative weekly measurement undoubtedly reflects the low water content of the tree trunk at some particularly dry period rather than growth. There are many definitions of growth and the majority incorporate the concept of new cell formation and/or increase in size. It is entirely possible that new cells might have been produced during the period when negative measurements were recorded with the dial gauge dendrometer indicating a possible limitation of this instrument as a dendrometer. As shown in Table I, it was

Table I. *A portion of the weekly growth table demonstrating variation in radial growth (growth is in thousandths of an inch)*

Tree no.	Position number	Week ending June 14	Week ending Aug. 2	Week ending Aug. 16	Week ending Sept. 13
1	11	− 9	0	−34	49
	13	− 2	2	−33	6
	12	−10	2	−32	38
	14	− 6	1	−44	47
2	21	15	15	−27	50
	23	−28	6	−25	52
	22	− 9	8	−42	52
	24	1	3	−47	46
3	31	−18	17	−34	27
	33	−14	3	−36	41
	32	−21	7	−40	51
	34	9	14	−30	49
4	41	26	14	−60	86
	43	−14	3	−60	92
	42	−20	0	−52	62
	44	5	3	−32	66
5	51	−24	−3	−26	33
	53	−13	16	−52	21
	52	4	6	−58	18
	54	3	19	−42	43
6	61	−10	7	−22	45
	63	− 4	16	0	12
	62	8	56	0	30
	64	29	66	−28	23

TABLE II. *Total growth (in thousandths of inches) according to the precision dendrometer for the period June 7–Nov. 1, 1947*

Tree no.	Position no.	Total growth	Average of systematic pairs	Average for the tree
1	11	80		
	13	59	70	90
	12	79		
	14	142	110	
2	21	104		
	23	80	92	106
	22	190		
	24	49	120	
3	31	141		
	33	158	150	141
	32	115		
	34	151	133	
4	41	217		
	43	244	231	175
	42	109		
	44	130	120	
5	51	98		
	53	17	69	74
	52	139		
	54	43	91	
6	61	139		
	63	155	147	165
	62	148		
	64	219	184	

found generally that all four measurements on a single tree would be positive or all negative although there were several instances where radial growth on one side of the tree was positive and on the other side it was negative. There was considerable variation in the magnitude of growth between systematic and random comparisons as can be seen in Table II.

Statistical analysis of the data (Table III) shows that there was as much variation within systematic as within random observations on the same tree. If only one dial gauge measurement is made per tree and the increase in diameter or circumference calculated from that, then no estimate of the error can be made. The variation in radial growth on the bole may be considerable (Table I). Therefore, it would be necessary to make several dial gauge dendrometer measurements at any given position on the bole in order to calculate the diameter or circumference as well as to determine the error of estimate.

Inasmuch as the mean square error within random pairs and within systematic pairs is of the same order of magnitude, they can be combined (Table IV) as the error to test the variation between trees and the difference in growth between trees is found to be significant at the 5 percent level.

SUMMARY AND CONCLUSIONS

Measurements on 6 loblolly pine trees were made, to test the dial gauge as a precision dendrometer. On each tree, 4 measurements were made weekly with a dial gauge to obtain both random and systematic comparisons. Considerable variation in the radial growth at the 4 selected radii were noted on each tree. Statistically it was demonstrated that the variation within random samples was of the same order of magnitude as within systematic samples, but that the variation between trees was significant at the 5 percent level.

If the dial gauge dendrometer is to be used

TABLE III. *Analysis of variance table to test variation within systematic pairs as compared to within random observations on the same tree*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value
Within systematic pairs	12	24,347.00	2,029.000	0.70*
Within random observations	6	17,485.00	2,916.250	

* Not significant at the 10 per cent level.

TABLE IV. *Analysis of variance table to test variation between observations on the same tree with variations between trees*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value
Between trees	5	34,218.5	6,843.9	2.94*
Between observations on the same tree	18	41,832.0	2,324.0	
Total	23	76,052.5		

* Significant at the 5% level but not at the 1% level.

for experimental purposes, it is suggested that several radii be selected at the same height above the ground on each tree so that the average diameter growth and an estimate of its error can be calculated. An alternative would be to take only one measurement per tree, but to measure a large sample of trees so that the average growth with its error of estimate can be calculated.

It is recommended that the word "precision" should not be applied to the dial gauge dendrometer since it is misleading and tends to give misplaced confidence in an instrument whose precision is limited as adapted for forestry purposes.

Acknowledgment

The author wishes to acknowledge the assistance of Dr. Paul J. Kramer, Department of Botany, Duke University, in obtaining all of the equipment and instruments used throughout this investigation.

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Harold E. Young

Forestry Department,
University of Maine,
Orono, Maine

TERRITORIAL AND SEXUAL BEHAVIOR IN THE GREAT INDIAN RHINOCEROS, A SPECULATION

The amount of information which is available about the life history, behavior and social organization of any one of the species of living rhinoceros is so scanty that no detailed or authoritative study is possible. This is a potential tragedy, as more than one of the five living species is threatened with extinction. *Rhinoceros sondaicus* Demarest, the Lesser One-horned Rhinoceros, apparently lingers in very small numbers only in west Java. *Rhinoceros sumatrensis* G. Fischer, the smallest of living species, is estimated (Ansell 1947) to number between 21 and 45 individuals in Burma with perhaps a scattering in Malaya, Sumatra, Indochina and Borneo. These species are particularly secretive forest dwellers, relatively inaccessible to an ecologist.

The Great Indian Rhinoceros, *R. unicornis,* on the other hand, lives in the open, in large park-like areas of swamp along the banks of the northern feeders of the Gangetic River systems in central Nepal, northern Bengal and Cooch Behar, and in Assam on either bank of the Brahmaputra River. A proper ecological study could and should be made of this species, of which Mr. Salim Ali and I estimated that there were just under 300 individuals left in 1949. Mr. Ali published an abstracted report on our findings for the International Technical Conference on the Protection of Nature (1950), in which he made a plea that a proper census and ecological study of this vanishing species be performed as part of the groundwork for any attempt at conserving these extraordinarily interesting animals. No action so far has been taken on this report by the Indian Government or other interested agencies, although the need remains great. Undoubtedly funds could be found for such a work provided an interested biologist would come forward to undertake such a study. The following tentative notes based on observations made in 1947, 1949 and 1950 are intended only as a suggestion and a potential line of thought about this fascinating problem.

The reason for the decline of all the Asian Rhinoceros species is the prevailing mythological belief, particularly among the Chinese, in the curative and aphrodisiac powers of rhinoceros horn, either powdered and taken internally, or rubbed against an affected part of the body, or indeed as a sort of talisman, used as a cup in votive ceremonies. In the latter form it would seem to be linked with the mediaeval European belief in the poison-sterilizing properties of a rhino horn cup for drinking. Other products such as blood and urine are sold as well, and the Calcutta Zoo finds a ready market for small bottles of urine from their captive *unicornis* at 14 annas (17 cents) each. Poaching of the three species of rhinoceros still goes on, although presumably the very decline in numbers of the species will make it increasingly unrewarding as an occupation. However, the political disturbances in Malaya, Java, Indochina and Burma with well-armed gangs using inaccessible trails in the jungles of those countries will undoubtedly be a continuing menace to the small *sumatrensis.*

Breeding

Scant data is available on the longevity or on the age at which breeding commences in the Great Indian Rhinoceros. A pair has been known to live 45 years in captivity. An age of 50–60 would seem a reliable guess, a comparable age to that of the elephant. As with the elephant, it could be presumed that a rhinoceros is adult by 12–15 years of age, although it may continue to grow after that. The gestation period is approximately 19 months (Ali 1927), and young at birth may weigh from 75–120 pounds.

From the above it will be seen that the female rhino cannot breed annually. Assuming a minimum lactation period of six months, a gestation period of nineteen months means that at the most a female in the prime of life could not mate more than every twenty-five months. Actually a cow rhino seems to keep her calf with her for far longer than six months. Perhaps three to three and a half years would be the shortest average time between breeding.

At present there is an adult pair in a roomy enclosure in the Calcutta Zoological Gardens. This pair has never bred because, as has been observed by the administering officials (personal communication), the female *or* the male may come into breeding condition, but so far their periods have not coincided. At one particular time the female may be in heat and receptive to the male, and at another time the male apparently comes into "rut," only to be refused by the female. From observations in captivity an unmated female will come into heat about once a year, and similarly a bull rhino will have an annual breeding or "rut" cycle. The length of this breeding cycle is uncertain but in captive animals it is only of a few days duration.

I cannot find any exact data on the time of breeding during a year. A pair that did breed in the Calcutta Zoo bred in March. The adult female at the Chicago Zoo has shown sexual excitement only once, in September, 1949, (personal communication). At the Kaziranga Sanctuary in Assam, the largest (164 sq. mi.) reserve for these animals in India, and the one with the estimated largest population (anything up to a figure of one per square mile of sanctuary area = maximum of 164), there are no accurate records of the breeding season. Young animals have been seen running behind their mothers in March at an estimated age of perhaps two months. This would mean a conception in June. Other young have been seen in January of a size to indicate a March mating. Mr. E. P. Gee reports (*in litt.*) matings in

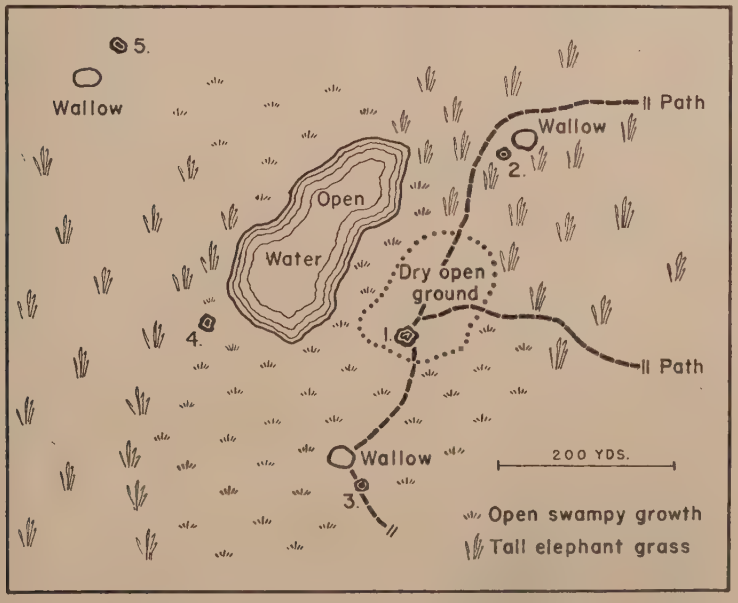

Fig. 1. Schematic diagram of a Great Indian Rhinoceros territory, showing central hard-trodden area, radiating paths, wallows, and central (No. 1), and outlying (Nos. 2, 3, 4) dung heaps. No. 5 dungheap and the wallow across the open water presumably belong to another animal.

February and April, and has seen newly born calves in November. All stages of slightly larger young have been seen in autumn, winter and spring, so that one can only presume that there is an extended and irregular breeding season with the spring months more generally favored.

Territory

The Great Indian Rhinoceros is noted for its habit of choosing a particular spot for the deposition of dung. These piles or mounds are usually in the center of a cleared area, and may be several feet high, perhaps three in the center, spreading outwards to a radius of four or five feet. Other smaller piles may be found on trails, in small clearings along trails or near wallows. The consensus of local opinion is that these piles are created by individual animals of either sex. The rhino is distinctly an unsociable animal. Two adults are never seen together except during a fight or when mating. The implication then is that these dunghills are territorial markers and that during part of the year each individual male or female rhino is king or queen of his or her own dung heap. The dung is deposited in balls about the size of a duckpin bowling ball, and the hill is created by the rhino's habit of slowly backing up to the mound in order to defecate.

The actual size of a territory seems to be a variable one. At Kaziranga there is one particularly favorable area along the bank of the Mora Diphlu stream where 14 or 15 animals may be seen in a morning's elephant ride. Elephants are used to get into rhino country here because of the great height of the grasses (up to 20 feet), the deep swampy streams and morasses, and the uncertain temper of the rhinos themselves. An average territory here would consist of perhaps 20–50 acres, usually near one of the *bhils* or swampy ponds, the shores of which are turfed with shorter grasses, on which, along with water plants, the rhinos graze. During the spring burning season, rhinos also graze on the tender young shoots of the heavy elephant grass, cane, and wild ginger, which form such a dense and enormously high growth most of the rest of the year. A typical territory then might appear somewhat like Figure 1.

Two rhinos may divide a *bhil* between them, apparently sharing opposite banks. Each rhino will have one or more wallows, on which it is dependent for a daily lubrication of the hide with liquid mud. In other parts of the Kaziranga Sanctuary, the size of the "territories" seems much larger. Rhinoceros may be one to a pond, or one to every other pond, or lacking altogether for a square mile or two for no readily observable reason.

Wandering

At certain times of the year the rhinoceros appears to wander far away from its haunts. During March, 1949, when Mr. Ali and I were studying the rhinos at Kaziranga, we continually visited old territories with old dung heaps dating back to the previous summer. The rhinoceros occupying each of these former territories had apparently moved somewhere else. At the same time we were told of an individual rhino which had recently swum across the Brahmaputra River to the north bank and had arrived in the Orang Sanctuary in Darrang District. All local observers were certain that the rhinos do move about periodically, although they had no specific data about the season. But it seemed significant to me that many of the animals were away from their habitual grounds during March in the middle of the supposed spring breeding season.

At this spring season, or at any rate when in mating condition, rhinos are said by the local inhabitants to emit a different call. Their ordinary notes are occasional grunts or low bellows of alarm or anger. The so-called mating call is a sweet high whistle, very penetrating and presumably capable of being heard for a long distance by another rhino. I have heard this sound only once, in March 1949, and was told by the mahout that it was a rhino. In addition, rhinos project their urine with great force backwards and may discharge it over quite an area of grass or trees. It seems safe to assume that it is an important recognition signal to these animals whose power of scent is well developed. By analogy with other mammals the urine during oestrus would doubtless be recognizable to the male.

Significance of Wandering

From the above scanty evidence, a supposition might be made that the Great Indian Rhinoceros tends to hold a territory during part of the year, but that at the onset of the rather indefinite breeding cycle, an individual may leave its territory and embark on a wandering migration, a *Wanderung*. Recognition apparatus is provided by the urine "sign," plus the high-pitched call. Since both sexes must be in an equivalent condition which persists only for a short time and is not adequately synchronized by the environmental cycle of the seasons, then males and females may have to wander very considerable distances in order to meet a physiologically-attuned member of the opposite sex. This is reminiscent of the condition in some of the *Mustelidae* (Marshall 1939). The very long gestation period, lasting well over a year, may be involved also in producing the irregularity of response to season changes. This wandering form of migration to secure a mating

would also tend to explain the occasional long-distance trips known to be performed by these otherwise territorial animals. From time to time, an animal will appear in an area in Assam where the species has not been recorded for many years. The small *R. sumatrensis* is also a great wanderer (Thom 1944). The only way in which such a speculation as the above could be proved or disproved would be of course by some method of banding or marking individuals. Meanwhile comments or added data would be greatly welcomed.

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S. Dillon Ripley

Peabody Museum,
Yale University,
New Haven, Connecticut

INSECT REMOVAL OF NITROGEN AND PHOSPHORUS COMPOUNDS FROM LAKES

The general features of the limnological cycle of nitrogen are known from the work of Mortimer (1938), and those of the phosphorus cycle from Einsele (1941), Hutchinson (1941) and Hutchinson and Bowen (1950). However an attempt has apparently never been made to include the role of aquatic insects in the conceptual framework of either cycle. This group has the peculiarity among lake organisms of spending the adult stage of the life cycle outside the hydrosphere. It is likely that many of the adult insects which emerge from lakes never live to return there, as Borutsky (1939a, 1939b) has shown for three species of Diptera from Lake Beloie. Since the adult mass is almost entirely derived from the lake bottom, a depletion of the chemical energy of the lake basin must result. It therefore becomes of interest to know the quantities of chemicals removed by adult insects, and the relations that these bear to the corresponding amounts sedimented. The present study was limited to analyses of total nitrogen and total phosphorus in freshly emerged adult insects from Lake Opinicon, Ontario. The author is indebted to Dr. H. W. Curran for permission to carry out the investigation at Queen's Biological Station.

Needham (1908) first devised a method of trapping adult insects as they emerged from a water surface. He named the pyramidal structure a tent trap. Modifications used by later workers have been given the names of Auffange-Netz or collecting net (Grandilewskaja-Decksbach 1935), emergence cage (Ide 1940) and Fangtrichter or funnel-trap (Brundin 1949). The general name of emergence trap is suggested for all devices designed to sample the emerging adults of aquatic insects, with a subdivision into floating and submerged types. The utility of the method has been discussed by Ide (1940) and requires no further comment here except to note that Macan (1949) found floating traps to act selectively in the collection of some dragonflies. Adults of *Pyrrhosoma nymphula* were never collected in Three Dubs Tarn by floating traps although the naiads were abundant in the bottom and adults did emerge elsewhere.

During the summer of 1951 a latin square experiment was designed and executed to test the hypothesis that floating emergence traps of different size and shape collect the same number and kind of aquatic insects per unit area of surface covered. A series of five traps was used in the experiment. The traps were arranged in the form of a circle in a shallow bay of Lake Opinicon, Ontario, at the location 24.4–12.6 on the bathymetric map of Lake Opinicon published by Curran, Bardach, Bowman and Lawler (1947). The results of that experiment will be reported at a later date. Interspaced among the five traps of unequal size and shape were five others, all cubical, each covering 0.25 m.^{2} of water surface. The collections from the latter were used for chemical analysis. The wooden framework of each trap was enclosed on the four sides and on half of the roof by a translucent plastic-coated screening. The other half of the roof was covered with a double layer of cheesecloth to permit air exchange. The traps were supported by 4 by 4 in. wooden floats in such a way that the bottom of each trap was 15 cm. below the surface of the water. Each float was tied to two poles which had been

pushed deeply into the mud. The vegetation in the bay was extremely dense at the time of the experiment. It consisted chiefly of *Potamogeton pusillus,* P. *Robbinsii, Vallisneria americana* and *Myriophyllum exalbescens.* The distance separating any two of the traps of equal size was approximately 17 m., and each stood above water 1.5 to 2.0 m. deep. The traps were

TABLE I. *Fresh weight, total nitrogen, total phosphorus and insects caught per trap of 0.25 m.² area*

Date of collection	Trap no.	Fr. wt., mg.	Total N, mg.	Total P, mg.	Number of insects					
					Tendipedidae	Other Diptera	Trichoptera	Ephemeroptera	Zygoptera	Total
July 2	1	1.7		0.005	14					14
	2	2.6		0.013	13					13
	3	11.6		0.025	23	1	1			25
	4	2.5		0.005	11					11
	5	2.2	0.117		13					13
July 3	1	10.3		0.027	23					23
	2	5.8	0.248		18	3				21
	3	9.0		0.024	22			1		23
	4	5.6		0.012	21		2			23
	5	15.1	0.543		36		1			37
July 4	1	19.0		0.038	34	1		1		36
	2	8.0		0.018	24	1	1			26
	3	19.6	0.580		18	1				19
	4	7.5		0.013	17					17
	5	13.2	0.450		28		1			29
July 6	1	10.2	0.363		26					26
	2	2.7	0.139		8					9*
	3	1.7		0.007	10					10
	4	34.1	0.823		16	3			1	20
	5	50.5		0.107	39		2		1	42
July 7	1	26.3		0.054	21	4	1			26
	2	13.9		0.020	17	1	1			19
	3	6.4		0.013	10	2	1	3		16
	4	6.8		0.016	17					17
	5	5.9		0.008	19					19
July 8	1	23.8	0.889		53	1		2		56
	2	9.7	0.339		21					21
	3	9.4	0.323		20	2	1			23
	4	33.1		0.057	24				1	25
	5	13.5		0.039	45		1	1		47
July 9	1	22.4	0.991		58		1	3		62
	2	8.7		0.025	33	1				34
	3	26.9		0.049	31			1	1	33
	4	6.4	0.300		28					28
	5	11.0	0.458		36					36
July 10	1	12.4		0.029	61		2			63
	2	140.7†	4.243		16	1	1			18
	3	5.2	0.255		17	1				18
	4	24.8	0.487		39	1				40
	5	17.9		0.037	53	1	1			55
July 11	1	18.2	0.708		80			2		82
	2	3.6		0.010	14					14
	3	22.4	0.775		36	1				37
	4	13.7	0.491		32	2				34
	5	16.2		0.033	59	1				60
July 12	1	30.6	0.824		98					98
	2	15.8	0.568		25	3	1			29
	3	20.4	0.749		57	1				58
	4	31.1	0.994		63	3	2			68
	5	34.2	1.043		119	1				120
Total		864.3	17.700	0.684	1616	37	21	14	4	1693
Average		17.3	0.708	0.027	32					34

* Includes 1 Hemipteran.
† Includes 1 *Phryganea* weighing 122.4 mg.

numbered 1 to 5 around the circle and were left in position during the eleven days which the experiment lasted. The insects were removed daily between 9 and 11 A.M. by lifting each trap into a rowboat, then crawling under the trap to collect the insects with a hand aspirator. The loss during collection is unknown but is estimated to have been less than 10%. Each sample was then transferred to a cyanide bottle and within two hours the fresh weight was determined to the nearest tenth of a milligram. After weighing, the samples were placed in clean screw-capped vials containing 70% alcohol. Both the insects and the alcohol were used for the determination of total nitrogen and total phosphorus.

Due to a severe rainstorm on July 4 (2.93 in. in four hours) the collection of July 5 could not be considered representative since there was heavy wave action inside the traps. The 50 samples which remained were randomly divided into two groups. In one of the groups total nitrogen was determined using the method of Boell and Shen (in manuscript) but modified for use in the range of 10 to 100 micrograms of nitrogen. Total phosphorus was determined according to the method outlined in Hawk, Oser and Summerson (1947, pp. 579–582) after digestion with sulfuric acid and hydrogen peroxide. Except for the Tendipedidae the insects were only identified to order. Table I shows the results of the analyses. Total N, expressed as a percentage of the fresh weight, varied from 2.0 to 5.3 with an average of 3.7%. Total P varied from 0.14 to 0.49% of the fresh weight with an average of 0.24%. The average daily fresh weight of insects leaving the water surface was 69.2 mg./m.^{2} The losses of total N and total P were 2.26 mg./m.^{2}/day and 0.15 mg./m.^{2}/day respectively. The N/P ratio in the entire collection was 15.1. The average water content of 3 species of adult Diptera cited by Buxton (1932) was 63%. Assuming the fresh weight of the present collection to be composed of 63% water and neglecting the ash, then the loss in terms of organic matter can be calculated to have been 25.6 mg./m.^{2}/day.

There was a large variation both in insects trapped on the same day at different locations, and at the same location on different days. To test whether these variations were significant an analysis of variance was applied to the data. The square roots of the total number of insects caught per trap per day were used in the analysis in order to reduce the spread. The data are summarized in Table II. Both location and time differences were highly significant. However when the same analysis was applied to the data from traps of unequal size and shape, F for locations was 4.09 (Probability < 0.01) and F for time was 1.90 (Probability > 0.05). Differences among locations therefore did exist.

TABLE II. *Analysis of variance of the square roots of the numbers of insects caught per trap per day*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F	Probability due to chance
Total	49	152.06			
Locations	9	79.24	8.80	9.47	$P<0.01$
Days	4	39.39	9.85	10.60	$P<0.01$
Error	36	33.46	0.93		

The shallow depth and thick spermatophyte carpet were perhaps the major agents in reducing pupal wanderings which otherwise might have obliterated the location differences. Little can be said concerning the time data since the weather conditions were not adequately recorded. However environmental effects on insect emergence do deserve comment. Scott and Opdyke (1941) found that the majority of Diptera emerged from Winona Lake, Indiana, from 6 P.M. to 12 midnight and from 4 A.M. to 6 A.M. in August. In the shallow water of Costello Lake, Ontario, Miller (1941) showed that the Tendipedidae emerged mainly from 4 A.M. to 7 A.M. in July, whereas over hypolimnetic water in September he found adults leaving the surface at all times of the day and night. Phillipp (1938) in an experimental laboratory study of the emergence of *Tendipes* (= *Chironomus*) *thummi* repeatedly observed emergence peaks between 8 A.M. and 12 noon and between 4 P.M. and 8 P.M. in March. These were occasionally replaced by one peak from 12 noon to 4 P.M. Phillipp (1938) found the emergence of *Tendipes thummi* to be augmented by an increase in dissolved oxygen. On the other hand, Miller (1941) suggested that the emergence of *Tanytarsus* sp. might be associated with a decreased oxygen and increased carbon dioxide content of the water. These results indicate differences worthy of further study.

Since organic matter containing nitrogen and phosphorus compounds is sedimented to the bottom of lakes, the question arises: What fraction of that sedimented is again removed by insects? To make such an estimate several assumptions had to be made since sedimentation was not studied in Lake Opinicon. Although the assumptions cannot be expected to hold rigidly, the final answer will serve to indicate the order of magnitude. The situation is fortunate in that both sedimentation (Scott and Miner 1936) and insect emergence (Scott and Opdyke 1941) have been studied in Winona Lake, Indiana. By applying the chemical data from Lake Opinicon to the emergence data from Winona Lake an estimate of the chemical losses may be obtained which can then be com-

pared to the corresponding chemicals sedimented.

The following assumptions were made:

1. Emergence traps accurately sample populations of emerging adult insects.
2. Of the insects trapped, 75% would normally never return to the lake from which they emerged.
3. The average weight per insect in the present collection was the same as in the collection of Scott and Opdyke (1941).
4. The annual emergence can be obtained by multiplying the daily average for July 1–15 by 120.
5. The average sedimentation of organic matter at a depth of 1 m. in Winona Lake (Scott and Miner 1936) was the same as that where Scott and Opdyke (1941) located their emergence trap over water 3 m. deep.

Assumption 1 has been disproven by Macan (1949) for dragonflies, and Scott and Opdyke (1941) found that darkened traps collected fewer adults than did more translucent ones. The extent to which this assumption is in error is unknown. Assumption 2 was based on the work of Borutsky (1939a, 1939b) who found that 90% of the dry weight of adult *Tendipes* (= *Chironomus*) *plumosus* which emerged from Lake Beloie failed to return to the lake. The corresponding amount for *Chaoborus* (= *Corethra*) was 55% and for *Tanypus* 80%. The average of the three figures, 75%, was selected as the best approximation. Assumption 3 is supported by the similarity in percentages of gross taxonomic categories in the present collection and that of Scott and Opdyke (1941). Assumption 4 is only a fair estimate. The actual emergence period is longer than 120 days, but is doubtless reduced in intensity in the very early spring and late autumn. Assumption 5 is probably in error also. The sedimentation at a depth of 1 m. may have been five times higher than the sedimentation at a depth of 3 m. in Winona Lake, but it is unlikely to have been more than that.

The average daily emergence at a depth of 3 m. for the periods July 1–15 of 1934 and 1938 in Winona Lake was calculated from the data of Scott and Opdyke (1941) to have been 152 insects per m.^{2} The corresponding number for water 1.5 to 2.0 m. deep in 1951 in Lake Opinicon was 136 insects/m.^{2}/day. The emergence calculated in terms of organic matter for Lake Opinicon was accordingly multiplied by 152/136 to obtain a comparable figure for Winona Lake. Granting the validity of the above assumptions it was computed that the insects which emerged from water 3 m. deep in Winona Lake in 1934 and 1938 removed an average of 2.5 g. organic matter per m.^{2} per year. The average organic matter sedimented at a depth of 1 m. (Collector Nos. 7 and 14) was calculated from the data of Scott and Miner (1936) to have been 902.5 g. per m.^{2} per year. Insects therefore removed 0.28% of the organic matter sedimented. Even if the calculation were ten times too low, the removal would still be too small to be of importance in the cycle of organic matter. This conclusion probably also applies to the cycles of nitrogen and phosphorus.

Summary

Populations of the adult insects which emerged from Lake Opinicon, Ontario, were sampled by emergence traps from July 1–11, 1951. The average daily emergence per square meter of lake surface was 136 insects which had a fresh weight of 69.2 mg. and contained 2.26 mg. total nitrogen and 0.15 mg. total phosphorus. On the basis of several assumptions it was calculated that the annual removal of organic matter from Winona Lake, Indiana, by aquatic insects formed less than one percent of the organic matter annually sedimented.

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J. R. Vallentyne
Osborn Zoological Laboratory,
Yale University,
New Haven, Connecticut

EFFECT OF PREGERMINATION TREATMENTS ON THE VIABILITY OF CEANOTHUS SEED

Ceanothus velutinus Dougl., or snowbrush, is one of the most widely distributed members of the genus and is common in the mountains from British Columbia and Saskatchewan to South Dakota and Colorado westward to California at elevations from 3,000 to 7,500 feet. Growing as a shrub 2 to 5 feet high with shiny, evergreen leaves, it occupies a wide variety of sites. It occurs frequently in small patches but often invades burned-over areas where it establishes itself densely to form the so-called "brush field." Snowbrush also reproduces on substantially disturbed mineral soils left by logging. Although *Ceanothus velutinus* is of little consequence for grazing by domestic animals, it is used slightly by mule deer.

Haupt (1951) found that snow in small openings of virgin forest occupied by *Ceanothus velutinus* was conspicuously high in water content in late winter compared to the snow in patches of mature and pole trees. Little information is available on the root systems of this shrub except that some of the main roots penetrate to depths of 6 to 8 feet and that, even in the case of the older plants, the root system extends beyond the (aerial) crown of the plant. Reproduction occurs both by sprouting and by seed.

In central Idaho, snowbrush is found throughout the range of ponderosa pine. It therefore provides competition in varying degrees with this important timber species. On old burns, where it may occupy the ground completely, it is an impediment in planting or seeding operations.

To learn the effect on the viability of the seed of treatments which simulated those commonly imposed by man in the woods, a germination test was made with seed collected at an elevation of 5,500 feet in the Boise Basin on the Boise National Forest. Only good seed as judged by external characteristics was used. The three major treatments were burning and abrading, together with a check. Burning consisted of placing the seeds in hardware cloth envelopes, burying them beneath 1 inch of moist mineral soil (which would not yield water when squeezed), and burning over them an 18-inch diameter brush pile continually stoked for 45 minutes. Abrading consisted of placing the seed in a metal container with 50 three-quarter-inch stones and shaking violently for 5 minutes. Half of the seed in each of the treatments in three replicates of 100 seeds each was placed in water heated to 180° F. and allowed to soak for 90 minutes as the water cooled. The other half was unsoaked. All six lots were then stratified in moist sand for 56 days at temperatures which ranged from 36° F. to 40° F.

The seeds were germinated in washed river sand in greenhouse flats under field conditions and watered each day for the 27 days of the test period. The number of seeds germinating out of the 300 in each treatment is shown in the following tabulation:

Group	Burn	Abrade	Check
Soaked	20	36	52
Unsoaked	21	3	1
Total	41	39	53

Analysis by Chi-square along the lines suggested by Snedecor (1946) indicates that the differences in the numbers which germinated within each group under the major treatments are not significantly different at either the 1 or 5 percent level of probability. The difference in the numbers which germinated for soaked and unsoaked seeds under the "abrade" and "check" treatments are significantly different at the 1 percent level of probability. The nullification of the effects of soaking by the burning treatment, implied in the tabulation, was also verified by a Chi-square test of interaction. Reasons for the low viability percentage as compared to those reported elsewhere (U. S. Forest Service 1948) can only be conjectured.

The results indicate that where *Ceanothus velutinus* seed lies in damp soils and far enough beneath the surface so that it is not consumed, fire can increase the germinative capacity of the seed.

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James D. Curtis
Intermountain Forest and Range Experiment Station,
U. S. Forest Service,
Ogden, Utah

A SIMPLIFIED APPARATUS FOR ORGANIC CARBON DETERMINATION BY THE WALKLEY AND BLACK METHOD

Many investigations of edaphic factors in conjunction with ecological problems are limited due to the equipment available and the time involved. The present paper reports on simplified laboratory equipment for the determination of organic carbon by the Walkley and Black method. The apparatus has been revised from that suggested by Piper (1944).

The principal problem involved in the determination of organic carbon is the preservation of the ferrous sulphate solution. This can be done with an arrangement that provides an atmosphere of hydrogen. Figure 1 is a diagram of a method devised for obtaining such a condition. The entire apparatus can be put together in a few minutes from standard pieces of laboratory equipment. Hydrogen is generated by a standard Kipp generator. The hydrogen flows from the generator (A), through the wash bottle (B), to the space above the ferrous sulphate solution in the stock bottle (C), and to the space above the solution in the burette (D). The stopcock on the generator is left open. In this way, additional hydrogen is provided which replaces that which is lost by diffusion through the connections.

The burette is filled by a siphon (E), without exposing the ferrous sulphate solution to the air, by opening the stopcock on the side arm. By using the described apparatus, the writers have been able to keep a ferrous sulphate solution for several months with no apparent oxidation of the solution.

A stock bottle of 2½ or 3 liters has been convenient in our work, although a larger bottle could be used if a great many samples were to be analyzed. Beakers with a capacity of 400 milliliters should be used for the analyses of the soil samples because they are large enough to allow the use of a stirring rod (F) which is driven by a small electric motor. The latter speeds up the titration process considerably because it eliminates the necessity for back-titration. The apparatus should be so constructed as to allow the use of a wooden block (G) under the beaker. By sliding the block from under the beaker, it may be removed without disturbing the stirring rod.

Other equipment which speeds the organic carbon analysis includes a laboratory pulverizing mill for the grinding of the soil samples and an automatic gravity-filling pipette for the addition of the potassium dichromate. A small, multiple hammer, motor-driven mill with a 30-mesh screen has proven very satisfactory for the grinding of the soil samples. The mill may be purchased from any one of several large biological supply companies.

The authors are indebted to Dr. L. M. Rohrbaugh and Mr. F. A. Rinehart of this department for their suggestions for the simplifying of the apparatus.

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Ralph W. Kelting
and
Elroy L. Rice
Department of Plant Sciences,
University of Oklahoma,
Norman, Oklahoma

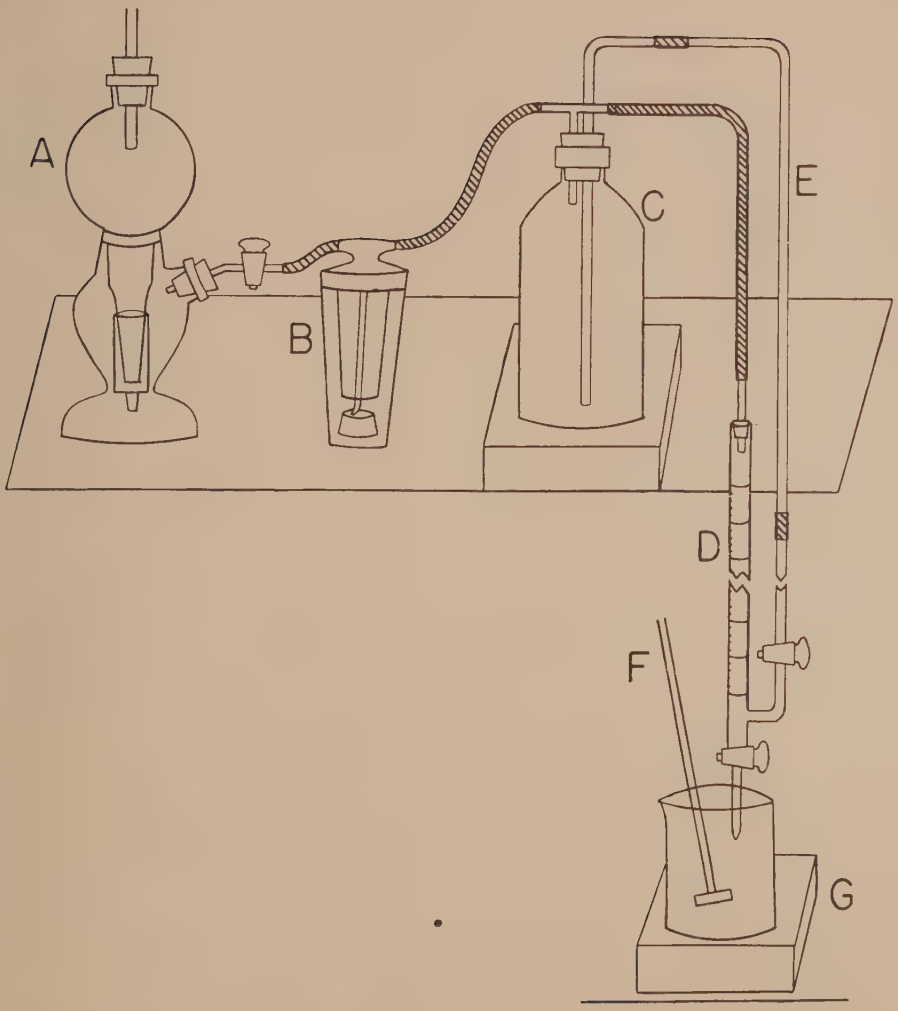

FIG. 1. Apparatus for the preservation of ferrous sulphate solution under an atmosphere of hydrogen gas. (A, standard Kipp generator; B, gas wash bottle; C, stock bottle for ferrous sulphate solution; D, burette with side arm for refilling; E, siphon for refilling burette; F, motor-driven, glass stirring rod; G, wooden block. All rubber connections are shown with hatched lines.)

REVIEWS

The Dusky-Footed Wood Rat[1]

This book represents a massive documentation of the life history of a single species of rodent in relation to its physical and biological environment. Meticulous field notes, gathered during 10 years of "nearly continuous" study by the authors and numerous associated investigators, are organized into 10 chapters. The book contains an enormous amount of information about most phases of the ecological life history of the animal studied. The most serious criticism is the lack of synthesis of the mass of material. One has the feeling of reading a carefully kept, well organized field notebook, but nevertheless a field notebook. The modern population ecologist will find it necessary to rework the data and make his own estimate of population parameters in respect to the various mensurable phenomena. This situation is unfortunate at a time when population ecology (as well as biological science in general) is struggling toward greater exactitude.

The habitat is treated in chapters II and III. Tabulations in which 100 homesites are classified according to, respectively, type of habitat, prominent vegetation, steepness of slope, type of support for houses, type of cover at the site, and screen from the side, give a comprehensive picture of the animal in relation to its vegetational environment. Descriptions of the species of plants that are most prominent in the environment of the rats are given from what is in essence the perspective of the rats themselves. Descriptions of 52 individual houses are tediously detailed and would have been better summarized.

Chapter IV is principally a list of animals associated in one way or another with the rats or their houses. Annotations present evidence bearing on the relationships of the associated animals to the rats. A "remarkably stable" population is pictured, in which replacement balances losses from disease, predation, and movement outside the area. Presentation of the evidence in support of the general conclusions that predation is more severe in areas of high population density than in areas of low population density but that the rate of predation tends to be constant even over a varied habitat would have been desirable.

Extensive data on behavior, food, reproduction and morphology are presented in chapters V to VIII. The evidence tending to indicate that "if a male remains within an area dominated by another male, he is not likely to attain his potential physical prowess" (p. 337) is of particular interest. The mating system is one in which promiscuity predominates. A male pairs with the most readily accessible female until gestation begins; he is then driven off and goes elsewhere in search of a mate. Replacement of population losses is effected through a long reproductive season which compensates for the small number of young per litter.

Chapter IX presents detailed accounts of changes in populations. The occupants of nearly 100 houses are tabulated for a period of seventeen months. The data conclusively demonstrate that a house exists much longer than any individual rat and may have several successive occupants. Changes in the occupants of individual houses are shown in a long series of diagrams showing the location of the respective houses on an area. The rats are highly sedentary. Nearly one-half of all movements of marked individuals were within distances of less than 100 feet, and approximately one-fourth more were within distances of 200 feet. There is an excellent discussion of social relations in the population. The great mass of tables, diagrams and half-tone illustrations breaks the continuity of the text material and would have been better placed in an appendix. The book is briefly summarized in chapter X.

This book contains an enormous amount of information about the ecological life history of the dusky-footed wood rat. As it stands, it is a book that every student of mammalian ecology or vertebrate population dynamics will want for his library. If the data had been analyzed statistically and if the authors had been willing to draw more positive conclusions from their information, it would have been a classic.

W. Frank Blair
Department of Zoology,
The University of Texas,
Austin, Texas

[1] Linsdale, Jean M., and Lloyd P. Tevis, Jr. 1951. The dusky-footed wood rat. vii + 664 pp., 384 figs. Berkeley: Univ. Calif. Press, $7.50.

Pollination in the Wet Subarctic [1]

It has been known since at least the time of Warming that in arctic and subarctic regions a much larger proportion of the angiosperms tend to be autogamous in their pollination (i.e., the stigma automatically receiving pollen by contact with anthers of the same flower) than is the case in Europe. The paper under review adds additional evidence for this generalization and further refines certain of our concepts of the biology of pollination. The study lends emphasis to a statement made by the author, "The somewhat schematic and stiff descriptions of conditions of pollination in certain textbooks should sometimes be taken with a grain of salt, and many of the classic observations of floral biology should be taken up for renewed investigations."

The Faroes, an island group located at about 62° N. latitude, present extremely unfavorable conditions for pollinating insects as a consequence of nearly continuous strong winds and rain. Since Hymenoptera and Lepidoptera are exceedingly scarce or absent, the only regularly entomogamous plants present are those few which can be pollinated by certain common flies or in a few cases by thrips. Consequently the only common method of pollination outside of autogamy is by wind, this being especially prevalent in the dominant grasses and sedges. Rain itself occasionally can be a pollinating agent. In certain insect or wind pollinated species geitonogamy (transfer of pollen between different flowers on the same individual) appears to prevail. In a few species, the dense inflorescence closes at night, the anthers and styles of adjacent flowers thereby coming in contact.

Autogamy, however, appears to be the most striking and universal adaptation to the unfavorable conditions for pollen transfer in the Faroes. This usually takes place by the dehiscing anthers coming into direct contact with the receptive stigma of the same flower, either before, during, or after anthesis. Many of these plants have flowers which are showy, fragrant, and provide abundant nectar, and which yet are almost never pollinated by insects in the Faroes. It is very significant, however, that many of the species which are normally autogamous in the Faroes may exhibit regular entomogamy and even be self-sterile in the European parts of their ranges. The author believes that this condition has resulted, in different species, either by the direct action of the Faroes' environment in modifying the phenotypic response of flower behavior, or by the development of races in the Faroes in which autogamy is genetically fixed and self-sterility absent or slight. It would seem that transplant experiments would be the logical method of differentiating between the genetic and environmental factors, and this procedure apparently was actually followed by the author in the case of one species.

Among the types of autogamy described is bud-pollination or the completion of pollination before anthesis. Autogamy after anthesis ("withering-pollination") occurs regularly in a few flowers, either obligatorily or perhaps facultatively, if other methods of pollination fail. Cleistogamy, in which the flowers never open, is represented by a small third group. The largest group of species in the islands, however, appear to be autogamous during the period of anthesis in which the flower is open, as a result of movements of stamens or style or their initial close proximity.

The author points out that the investigator should be attentive to the question of whether species considered autogamous really produce viable seeds or not. Hagerup has apparently, however, limited his own observations of fruit and seed production to whether this is fairly abundant or sparse, regardless of the viability percentage. Furthermore, the possibility of apomixis occurring, either in the presence or absence of pollinating mechanisms, is not even mentioned.

The publication is profusely illustrated with drawings of the flowers of most species discussed. A very useful and commendable feature is the index to genera which are mentioned in the text. Altogether, species representing 57 genera are mentioned. The English translation of this work is very welcome indeed, and in only a few spots does imperfect translation make the meaning of the author uncertain.

John Pelton

Dept. of Botany,
Oberlin College,
Oberlin, Ohio

[1] **Hagerup, O.** 1951. Pollination in the Faroes—in spite of rain and poverty in insects. Dan. Biol. Medd. **18** (15) : 1–48. Ejnar Munksgaard. Copenhagen. $1.00.

The Journal of Human Ecology

A new journal in the field of ecology has recently made its appearance. This is the *Journal of Human Ecology* which carries the explanatory subtitle, "The study of the influences of

environment upon human behavior." It is published for the Weather Science Foundation by Weather Forecasts, Inc., Crystal Lake, Illinois. Raymond H. Wheeler, Chief of Staff, Climatic Research Division of the Weather Science Foundation, and Head of the Psychology Department, Babson Institute of Business Administration, Wellesley, Massachusetts, is the editor. The managing editor is Sydney D. Thompson, also of the Weather Science Foundation. Articles appear as separate units planographed on unbound sheets $8\frac{1}{2} \times 11$ inches in size. The first three parts of volume 1, number 1, are devoted to a discourse on "Aims and Policies" prepared by Dr. Wheeler. The scope is extremely broad, including all phases of human activity as related to environmental factors. Attention will be given to both purely scientific investigators and practical applications of external relationships to human affairs.

Physical geography, climatology and climatic cycles, physical and chemical conditions of existence, relations of living organisms to each other, and social and economic factors in relation to man will be included. These fields are to be considered in the widest sense. Social and economic factors, for example, will include aspects of health, psychology, political science, business, history, religion, and the arts. The five basic divisions organized at the present time are as follows: 1. Business and economics; 2. Psychological; 3. Biological and medical; 4. History and political science; 5. Climatological and miscellaneous problems in relation to human behavior. The editor will welcome manuscripts from any field of scholarship which touches upon the relation of human activity to environmental conditions. Manuscripts should be sent to the editor. Correspondence pertaining to subscriptions should be sent to the managing editor, Weather Science Foundation, Williams and Brink Streets, Crystal Lake, Illinois. Subscription rates are $15.00 per year for libraries and academic personnel, otherwise $25.00 per year.

The present Board of Associate Editors [1] includes: Warren D. Allen (music and history); Ernst V. Antevs (geology and climatology); S. Howard Bartley (psychology); Konrad Buettner (geophysics and bioclimatology); Ralph W. Dexter (biology and bio-ecology); Leo S. Hellmer (animal behavior and climate); Nicholas Rizzo (medicine and psychology); Frederick Sargent II (physiology, medicine, and bioclimatology); Winifred J. Sawtell (astronomy and climatology); A. Thornton Steele (economics and business); and Stephen S. Visher (geography and climatology). The first volume was dedicated to the memory of Dr. William Ferdinand Petersen "a great pioneer in the field of human ecology," who had accepted a post on the Board of Associate Editors shortly before his death. Vol. II is dedicated to the late Dr. Ellsworth Huntington of Yale University, eminent economic geographer and second president of the Ecological Society of America.

Ralph W. Dexter
Department of Biology,
Kent State University,
Kent, Ohio

[1] Cleta Olmstead Boughton (archeology and history of art) and Roy I. Wolfe (geography and human ecology) are also serving on the Board of Associate Editors.

Ecological Crop Geography and Field Practices of Japan, Japan's Natural Vegetation, and Agro-Climatic Analogues in North America [1]

This study on Japan is another contribution of the American Institute of Crop Ecology dealing with crop ecology and North American agro-climatic analogues of various countries. This study presents detailed data on climate, soils, natural vegetation, crop distribution, performance of varieties, field practices, control of plant diseases and insects, and a description of the agro-ecological regions of Japan. Climatic and latitudinal data of 150 weather stations of Japan are compared with similar data in America to delineate analogous areas. The main climatic records utilized are mean monthly and yearly temperatures, maximum and minimum temperatures, average monthly, seasonal and yearly precipitation and relative humidity, precipitation-effectivity indexes and ratios (Thornthwaite's method), length of frostless seasons. Tables and maps are used to show these data and to pinpoint the North American climatic counterparts of each area of Japan. For example, Tokyo is shown to have as its closest counterpart the vicinity of Roxboro, North Carolina.

Due to the ruggedness of the mountain-and-hill country of Japan, less than one-sixth of the land area is under cultivation. The great popu-

[1] **Nuttonson, M. Y.** 1951. Ecological crop geography and field practices of Japan, Japan's natural vegetation, and agro-climatic analogues in North America. 213 pp., 22 figs., including maps. American Institute of Crop Ecology. Washington, D. C. $4.00.

lation pressure has been in part responsible for the relatively high food production from the limited area of arable land. This high production has been obtained by use of improved crop varieties, by means of extensive and heavy applications of fertilizer, by careful control of plant diseases and insect pests, by efficient practices such as multiple-cropping, and by careful irrigation in the case of rice, the most important crop.

This type of study for any country is of especial importance now to the United States, inasmuch as agricultural specialists familiar with American production find themselves in foreign areas lacking scientific information as to varieties and practices most suitable to those areas. It is of great value to a technician to know that the particular area of concern to him in a foreign country is closely analogous to a given area in the United States or in some other agriculturally well-developed country with which he is already familiar or with which he could become familiar through literature and correspondence. An American expert in Osaka, Japan, for example, could do his work with greater assurance if he knew that climatically and ecologically he faced a natural environment not too much unlike that of Greenville, South Carolina. He would then have a much better idea as to what varieties to select, what insects and diseases to anticipate, and how to control them, and what water and soil conservation methods might be most appropriate.

However, the ascertaining of the American analogous areas does not give enough background for some of the tasks which the United States Point IV administrators and the Mutual Security Agency have set up for themselves. In addition to knowing American agro-climatic analogues of a given country, the technicians should be provided with a list of analogous areas in other agriculturally well-developed countries of the world. An agricultural specialist assigned to a given locality in India, knowing only that his area is analogous to Gainesville, Georgia, is not as well-armed as he might be if he knows also that his area is analogous likewise to Kumamoto, Japan, where a similar plentiful supply of labor exists and where land is scarce and where production per acre is far better than in Georgia.

It is possible to equip each expert in a given area with knowledge of the agricultural systems, practices, varieties, etc., of each of the successfully developed areas analogous to the area in which he is working. In this way, in a relatively short time, the real values of good experimental studies, better varieties, and field management practices can be made available to the specialist so that he can select from anywhere in the world the most suitable plant material or practices for his locality. Until such knowledge is available, the expert assigned to a new area is at a great disadvantage as he cannot avail himself of the "know-how" and experience developed within ecologically similar areas. He would require a considerable period of time for testing a multitude of varieties and field practices until, by trial and error, he might find something suitable for his area.

Additional studies of this kind are needed greatly at this time. The abundance of highly useful experimental data in the United States and Japan, for example, could be placed at the disposal of under-developed areas in India, Iran, Formosa and other Far Eastern and Middle Eastern regions through the ascertaining of agro-climatic analogues. It is important to make a detailed study of the agro-ecology of well-developed tropical areas of the world so that the agriculture of these areas, carefully described, might help in the development of climatically similar under-developed areas. India, southeast Asia, Indonesia, the Middle East, and Latin America are some of the important regions that could benefit from a detailed study of their own agro-ecological conditions and the ascertaining of climatic analogues in better-developed regions. The agro-climatic analogue approach is sound ecologically and agronomically for providing a shortcut in introducing suitable varieties and field practices, and for limiting the number of varieties and practices under experimentation. This is especially valid for countries urgently in need of crop improvement and greater food production, which countries usually lack technical personnel and facilities for independent original plant-breeding and crop-improvement programs.

Herbert C. Hanson
Department of Biology,
The Catholic University of America,
Washington, D. C.

Animal Chromosome Numbers [1]

The second edition of Makino's valuable list of chromosome numbers, now published for the first time in the United States, provides information concerning 2754 invertebrate and 563 vertebrate species, together with bibliographical references which on the whole are remarkably complete and up to date. As might be expected more than half the species listed are insects.

[1] **Makino, Sajiro.** 1951. An atlas of the chromosome numbers in animals. xxviii + 290 pp. Ames, Iowa: Iowa State College Press, $5.00.

Next to the Acrididae, the largest single family represented is the Drosophilidae which occupies twelve pages, even though a considerable number of the newer species have not been included.

The arrangement is systematic down to families which, together with genera and species, are listed alphabetically for ease of reference. In the case of the Drosophilidae, unhappily, this is departed from in favor of the karyotype classification of Metz and Kikkawa & Peng which, whatever its previous merits, is no longer a useful scheme and should have been supplemented by arrangement according to sub-genera and species groups. The valuable paper of Wharton (Univ. of Texas Publ. No. 4313) on Drosophila karyotypes is not cited, although the more recent one of Ward (Univ. of Texas Publ. No. 4920) is included.

No present day cytologist is more aware of the gaps in our knowledge of the comparative karyology of animals than Makino who, with his students and colleagues, is actively engaged in reducing these gaps. The next edition of this atlas is bound to evidence an even larger proportion of contributions from his laboratory.

This book belongs in every zoological library where it will provide not only information, but also stimulus to further work. The fact that we have information concerning the chromosome numbers of less than 4,000 of the described species of animals may seem discouraging to some biologists, but it may prove a powerful stimulus to those who realize that the study of chromosome physiology and evolution is only now in its infancy.

D. F. Poulson

Yale University,
New Haven, Connecticut

Turtles [1]

This handbook, written by one of the best authorities on turtles in our country, treats the species and subspecies which occur in the United States, Canada and Baja California. Ecologists will be interested in the discussions of the physiology and behavior of turtles in general in the introductory part of the book and in the material found under such headings as habitat, habits, breeding, feeding and economic importance in the separate accounts of the 79 species and subspecies listed. There are keys to the families, genera, species and subspecies as well as descriptions of each form. Geographic ranges are described for each species and are outlined on maps for all except the sea turtles. The information on the lives and economic importance of turtles is augmented by the author's critical judgment as well as his rich experience both in this country and in Latin America. The author's tangential digressions will not dismay the stout-hearted, and will tickle the fancy of many readers. The bibliography is practically complete through 1949, but, due to the exigencies of publication deadlines, several important later papers have not been utilized in the text (*e.g.*, Lucille F. Stickel's studies on populations and home-range relationships of the box turtle).

This book deals more extensively with the origin, physiology and anatomy of turtles than does Clifford Pope's "Turtles of the United States and Canada" (1939). Likewise, systematic relationships and the problems related thereto are more heavily emphasized. And, since 13 years separate the publication dates of the two books, it almost goes without saying that a nomenclatural shuffling has taken place. Carr's book does not supplant or outmode Pope's; it is merely different. Pope's emphasis is on habits and his book serves as an excellent introduction to the turtles of the area covered; Carr's more nearly equalizes the emphasis on systematics and habits. Carr's work is more technical (to be sure, there are many light moments!), more thoroughly documented and thus intended for the scientific investigator as well as the lay naturalist; Pope's is definitely directed toward the latter. Carr's bibliography contains references to all literature consulted, again a valuable adjunct to the scientific reader; Pope's is selective, containing only those references that he considers most important. In other words, they are both fine books and not subject to comparative evaluation because of the difference in intention. Both of these liberally illustrated (the halftones are somewhat better in Pope) books should be on the shelves of every ecologist; Pope's should precede Carr's on the beginnner's.

Norman Hartweg

Museum of Zoology,
University of Michigan,
Ann Arbor, Michigan

[1] **Carr, Archie.** 1952. Handbook of turtles. xv + 542 pp., 37 figs., 82 pls., 23 maps. Ithaca, N. Y.: Comstock, $7.50.

Feeding the Underfed World [1]

To the problem of the world's expanding human population and its correlative poverty, the geographer's eclectic experience is, and should be even more so, an informational warehouse. When, as in the last war, Dr. Stamp's Land Utilization Survey of Britain became extremely valuable both for military purposes and for increasing agricultural production, it appears that ostensibly academic natural resource studies are being recognized for the practical purpose of saving man from his own species.

The blatant chauvinism inherent in the "Point Four" and other aid programs to "underdeveloped" countries is illuminated by this objective approach to the problem as a whole. In the light of our superior but unapplied knowledge of temperate-climate agriculture and the comparatively low American and Australian crop yields per unit area, it becomes appallingly clear that *we* are the underdeveloped countries. Moreover, we would seem to be foisting our ready-made, exploitive, big-machine practices on peoples and lands to which they may mean disaster. The example of the English gentleman who retired to Ceylon with his British stock, crops, machinery, and hunting hounds, only to be broken by the alien environment, is fraught with political and economic implications. To ignore them, Professor Stamp points out, is to court the kind of defeat that cost the British £36,000,000 in the African groundnuts plan.

Half of this excellent little volume is a sort of stock-taking of people, food, land, and minerals. Our vast ignorance concerning the clearing and managing of tropical lands, the climatic obstacles and distribution of tropical peoples, lead to the conclusion that the world's hope for increased food production does not lie in opening the equatorial forests, or even in the more likely savannas, but in increasing production where cultivation has already determined the landscape character. The demographic discussion is more than adequate; those who have not thought deeply on the matter may be surprised to learn that the Caucasians are the expanding populations of the world. The Western problem is very different from that of peoples already living up to the land's carrying capacity in India and China, and the author tends to agree with Dr. Black of Harvard that each nation must, for the most part, work out its own problem.

But in the second half of this study, which tends neither toward panic nor complacency, Dr. Stamp urges world land planning, and, in fact, land use patterned after northwestern Europe's "well balanced, mixed agriculture, based essentially on rotation of crops and on the coordination of arable farming with stock rearing and feeding."

Goat keeping, and nomadism in general, are too expensive and inefficient for existence in the envisioned reclamation. The vicious circle of poverty, based on such practices as goat-herding in the Middle East, the burning of cow manure for fuel in India, and the counting of wealth by the cow in Africa, can be broken by applied ecology, but only with a great deal of anthropological and sociological information.

One of the least obvious and yet most laudable effects of "Land for Tomorrow" is that it shows what *Fortune* magazine calls "Malthusian Mischief" to be a straw man. The editors of *Fortune* view the "neo-Malthusians" as wet-blankets and pessimists. The objects of their vituperation are uncomfortably close to the conservationists and others who would plan for the future. Neither Malthus nor those who currently recognize the validity of his thesis have predicted that man will crowd himself off the planet, nor has Dr. Stamp written off civilization.

It is indicative of the perspicacity of "Land for Tomorrow" that the defects that appear are mostly found in its omissions. However, "man's struggle against nature" appears several times. In the light of our present approach this concept is somewhat obsolete; as a picture of man in the landscape it is stereotyped and apparently as embedded in the thinking of many scientists as it is inapplicable to an objective description of the whole biota. The short discussion of pest control suffers somewhat from the same defect. There is a short, unsatisfactory chapter on the potential of the sea for feeding future human generations, and there is little or no mention of birth control in Asia's or Africa's futures.

But this writer's only serious quarrel is with the author's conclusion that the world can support a population of ten billion people. Nowhere in the book is it suggested that along with stock-taking of people, land, and food, it might be wise to take stock of the imponderable elements, particularly the aesthetic factors that enable man to live in health. It seems probable that ten billion people are more than we can stand to have around, regardless of how well fed they are.

Paul Shepard, Jr.
Conservation Program,
Yale University,
New Haven, Connecticut

[1] **Stamp, L. Dudley.** 1952. Land for tomorrow. The underdeveloped world. 230 pp. Bloomington: Indiana University Press. $4.00.

A Textbook of Animal Ecology [1]

Unlike most fields of biology, ecology is not overabundantly supplied with textbooks. W. H. Dowdeswell, senior biology master at Winchester College, has not aimed at the digestible version of the Chicago treatise that is so badly needed, but has produced a modest and wholly admirable work designed "for use by school Sixth Forms and first year University students." American students can use it with profit, but probably will not do so to any noticeable extent, for in terms of the pattern of American education it falls inevitably between two schools. The book is too slight to be suitable for an advanced college course in ecology, whereas students in the large public secondary schools are too busy with more important things, like home economics, to take a formal course in anything so recondite as animal ecology. Such a course, using such a text, might be an ideal substitute for the showcase courses in general biology inflicted on thousands of American college freshmen, but no publisher of freshman textbooks is likely to place his bets on that remote possibility.

The need for a college textbook of animal ecology is so great that American ecologists engaged in teaching the subject in college, or who are waiting for the right textbook before offering the course to advanced undergraduate students of biology, will undoubtedly consider Dowdeswell's book seriously. They may not find its slightness a fatal defect. What is in the book is sound; it is an introductory account, rightly emphasizing the structure of biotic communities, but not neglecting parasitism, symbiosis, animal behavior, ecological zoogeography, or evolution. The style, though humorless, is direct and not at all condescending, and while it is an easier book to read than Borradaile's "The Animal and its Environment," it covers much the same ground in a way that shows much more ecological flair.

What is left out, unfortunately, is the aspect of ecology that makes it more than systematized natural history—the quantitative approach. In the last chapter, called *practical ecology* (somewhat misleadingly, since it offers suggestions for field and laboratory work and has nothing to do with applied ecology), directions are given for estimating population size, and even for testing results statistically. Few hints are to be found elsewhere of ecologists' reasons for making such estimates; the word "productivity" does not occur, nor is there any discussion of mortality and natality rates or of age distributions within populations. The attention paid to gene distributions within populations stands out by contrast. No doubt productivity and population dynamics are matters too abstruse for elementary students, though it strikes one as remarkable that such students are expected to be able to titrate and to build a Wheatstone bridge, but the stripping-down process has gone much farther than seems really necessary—physiological problems at least as difficult as the synecological ones that are omitted are treated with an almost complete avoidance of graphs and tabular data.

In brief, the book has the defects of its qualities. It would be suited to American college freshmen, but is intended for a rather different group of students. Despite its simplicity and despite its concentration on animals and environments peculiar to Great Britain, it could even be used as the skeleton of a more advanced course in an American college, for it provides an extensive and carefully chosen bibliography not by any means confined to popular works. One can only hope that when the long-awaited college textbook of animal ecology is written it will be as free from errors and as stimulating to its users as this book should be to the gifted members of British Sixth Forms.

E. S. Deevey
Osborn Zoological Laboratory,
Yale University,
New Haven, Connecticut

[1] **Dowdeswell, W. H.** 1952. Animal ecology. xv + 207 pp. London: Methuen. 12s. 6d.

Human Paleoecology [1]

Archaeology has been defined as "the art of using the unverifiable to deduce the unwarrantable about what probably never happened," or "the study of the incredible by the credulous." In the hands of its practitioners, at least of those among them who write, it can be the drearest of subjects, and when life is breathed into the prehistoric past it is usually by gifted amateurs whose imagination outruns their science. The sympathetic view, that archaeology is human paleoecology, is reiterated but seldom demonstrated by the professionals. The general ecologist, clinging stubbornly to that view despite rebuffs, will henceforth find it more easily defensible, for Grahame Clark has written an absorbing and satisfying book on the economic aspect of European paleoecology. Tightly

[1] **Clark, J. G. D.** 1952. Prehistoric Europe. The economic basis. xix + 349 pp., 16 pls. London: Methuen, £3; New York, Philosophical Library, $12.

packed into more than 300 small-quarto pages, this is what archaeology should be but hardly ever is. The author, who has recently been appointed to the Disney chair of archaeology at Cambridge University, is a distinguished student of mesolithic cultures and their adaptation to the changing environment of northern Europe during the Boreal phase of returning forest, and is currently directing a spectacular excavation at Star Carr in Yorkshire.

Standard works on archaeology normally have what teachers of comparative anatomy call "horizontal" organization. Ancient cultures are described as wholes, as nearly as the evidence permits; the objective is to show how cultures succeeded each other in time, and were related to each other in space. This is not a bad organization in itself, but it can lead to monumental dullness. Only rarely, as in Vaillant's "Aztecs of Mexico," does the tangible evidence justify an ecologically satisfactory reconstruction of the unity of a culture; preoccupation with methodology usually transforms such attempts into deadly discussions of stratigraphy and artifact typology.

By contrast, Clark's book has "vertical" organization. The time-range considered as "prehistoric" is postglacial in the widest sense, *i.e.* from late upper paleolithic (Magdalenian) to iron age, or to the time of direct influence by literate (historic) civilization. Within this span of approximately 13,000 years the chronologic-stratigraphic framework is taken almost for granted, and no attempt is made to describe in detail the various phases of mesolithic, neolithic, bronze age and iron age cultures. Instead, the elements of material culture are examined systematically, beginning with the arts of hunting and fishing, passing through pastoralism, agriculture, and metals technology, and ending with travel and trade. For the ecologist as well as for the general reader this organization has the great virtue of keeping function always to the fore; the question invariably asked about an artifact is, "how was it used?", not "by what features shall the archaeologist classify it?" How refreshing this can be may be judged from the fact that the discussion of pottery is confined to two pages. Apart from its readability, however, the book is a work of prodigious scholarship, for what Sollas did for paleolithic man in "Ancient Hunters," Clark has done in a vastly more complicated field.

In reviewing a book so crammed with information, almost all of it brought together for the first time, it is impossible to discuss details. A few high spots of ecologic interest may be mentioned, more to give the flavor of the work than by way of summary, for it really is "all summary." Honey was gathered already in upper paleolithic times in temperate Europe, and a charming rock-drawing from eastern Spain shows a steatopygic lady, armed with nothing but a bucket, in the act of doing so; the bees are definitely tetrapterous. The camps of the Hamburgian reindeer hunters on the north German plain (tundra, as it was then) were summer camps; this is shown by the interrupted size-frequency distribution between the calves and yearling reindeer, as well as by the occurrence of summer visitors among the fossil migratory birds found in the middens. It even seems possible, though Clark does not say so, that the Hamburgians were the "summer form" of migratory people who wintered in caves in the south of France and have long been known as Magdalenians. Oats and rye are believed to be mimies (under cultural selection) of emmer and of wheat or barley, respectively, and to have become crops in their own right only as a result of the sub-Atlantic climatic deterioration of about 600 B.C. The amber that was prized by the Greeks in Mycenean time (c. 1500 B.C.) was Baltic amber, as shown by its high content of succinic acid; the author does not tell us whether the twice-fossilized resin contained fossil arthropods.

No mistakes have been detected, but the work has two sorts of deficiency. Only the first can fairly be called a defect: conventional archaeology has been too much slighted and the totality of cultural activity fails to come through clearly. There is a correlation diagram, an exceptionally ingenious one, with dates along one axis; nowhere in the book, however, can one find exactly where and when most of the peoples referred to lived, and what their cultures looked like. This is of course a defect that follows directly from Clark's "vertical" treatment of technology, and while it can easily be repaired by resorting to such works as that of Hawkes,[2] it would seem that a few more pages of the introduction could well have been granted for a chronologic and geographic synopsis.

The other deficiency is not a real defect, because it is implicit in the subtitle, "The economic basis." Those ecologists who look for a unified treatment of *all* aspects of human paleoecology will not find it in this book, or in any other. Little is said of population size or other demographic matters, and still less of those intangible aspects of human behavior that are unrepresented, or of speculative significance, in the cultural fossils that have been excavated. Art, for example, is not discussed, and, had the au-

[2] **Hawkes, C. F. C.** 1940. The prehistoric foundations of Europe. To the Mycenean Age. xv + 414 pp., 5 folded plates. London: Methuen.

thor had occasion to mention "the harp that once in Tara's halls the soul of music shed," one feels that he would have restricted his remarks to the wood and gut of which it was made. Having registered this mild complaint, one must hasten to say that the definitive human paleoecology could not possibly be written yet by anyone. When it is written it will lean heavily on Clark's masterly summary of the economic foundation of European prehistory.

E. S. Deevey
Osborn Zoological Laboratory,
Yale University,
New Haven, Connecticut

Vertebrate Sexual Cycles [1]

The discovery that length of day is an important regulatory factor in reproduction, and the advances in our knowledge of hormones during the last three decades have stimulated much research on the problem of sexual cycles. The stated purpose of the present volume is the presentation of "a brief but up-to-date account of our knowledge of the sexual physiology of vertebrates." The author, however, has not restricted himself to the purely physiological aspects of reproduction. In reality, this book is an examination of the seasonal reproductive cycles and estrous cycles of vertebrates and an attempt to analyze "those factors which are now thought to determine, control, or affect them." Since environmental factors are important in the regulation of breeding cycles, the problem is of particular interest to ecologists.

In Chapters 1 and 2 (pp. 1–19) annual cycles are defined and considered in relation to latitude and domestication. This is followed by a definition of estrous cycles and a discussion of their relation to annual breeding cycles. Chapter 3 (pp. 20–44) is entitled "The Environment and Reproduction" and comprises about 25% of the book. Bullough, following Baker, concludes that the breeding seasons of most vertebrates are determined by two sets of causes—the ultimate and the proximate (p. 43). "The ultimate causes of the timing of a breeding season are the reasons why that time of the year is the most beneficial for this purpose. Probably the most important single reason is that the food supply should be adequate both in quantity and quality to satisfy the extra needs of the young when they appear." The proximate causes are three-fold: the "internal reproductive rhythm," the "environmental variant (sun, moon, rain, etc.) to which the cycle is attuned," and the "group of factors in the immediate neighborhood of the individual animal (the breeding area, the mate, and perhaps the social group)." One of the weaknesses of this chapter is the author's failure to make a distinction between the potentiality to breed and actual breeding. Hence, the relation between the factors which regulate gametogenesis and those which regulate breeding (when mature gametes are present) is not always clear. Chapter 4 (pp. 45–79), entitled "Hormones and Reproduction," reviews some of the aspects of reproductive physiology and attempts to correlate the physiological and environmental factors which regulate reproduction. The author concludes that the anterior lobe of the pituitary is a control center of the reproductive processes and "the intermediary between the external environment and the nervous system on the one hand and the maturation and proper functioning of the gonads on the other." In Chapter 5 (pp. 80–95), there is a brief presentation of the relation of hormones to sexual behavior, including some comments on bird migration. The concluding chapter (pp. 96–98) is devoted to general conclusions and is essentially a succinct summary. A glossary, a list of species mentioned (with scientific names), a bibliography of 203 titles, and an index conclude the book.

It is unusual to find a synthesis of the physiological, psychological, and ecological aspects of such a broad biological problem as sexual cycles. The author's interest lies unquestionably in the broad view of the problem and especially in the evolution of physiological mechanisms. His attempt to integrate the details of several diverse fields should prove useful in providing an awareness of the many facets of the problem of sexual cycles. The book only achieves in part its stated purpose of introducing the main facts and theories and, hence, presenting an up-to-date account of our knowledge of sexual cycles. This is due partly to the brevity imposed on the author and the unavoidable delay between completion of the manuscript in September, 1949, and its publication in December, 1951. (The bibliography includes few references after 1947, and a number of relevant papers published well before that are not cited.) However, these are minor criticisms. The primary reason for its failure to achieve its stated purpose is that too frequently in the text it is difficult to distinguish between fact and theory, the personal opinions and interpretations of the author, and the conclusions of other investiga-

[1] **Bullough, W. S.** 1951. Vertebrate sexual cycles. VIII + 117 pp, 12 text-figs. London: Methuen; New York: John Wiley. $1.50.

tors. In the opinion of the reviewer, this is a serious shortcoming for a book of this type. The author was aware of the problem, for he writes (p. 79) : "In handling such an abundance of evidence, most of it inconclusive and much of it contradictory, it is impossible to do more than to pass a personal opinion as to what is significant and reliable. Another, judging the same case, may be found to lay stress on different parts of the narrative and even in some particulars to arrive at different conclusions." The reviewer does not take issue with the author's stand on this matter or with many of his opinions and conclusions, but he feels that the reader should be informed of the reasons for the author's opinion and particularly the scope of the evidence examined. Above all, the reader should be able to distinguish between the facts and interpretations presented by the original investigators and those of the author.

Albert Wolfson
Department of Biological Sciences,
Northwestern University,
Evanston, Illinois

Clapham, A. R., T. G. Tutin, and E. F. Warburg. 1952. *Flora of the British Isles.* li + 1591 pp., 79 figs. Cambridge: The University Press. $9.50. Three British botanists, with a modern outlook, have cooperated in the writing of this, the first comprehensive new British flora to appear in more than half a century. One might suppose that in so small an area as the British Isles, with so dense a population, the flora would long ago have been completely known and adequately described. Actually, during the past 50 years many distinct species, subspecies, and varieties have been discovered, and at the same time, much new knowledege has been gained about many well-known species, especially in regard to their genetics and ecology.

This work contains keys to the families, genera, and species as well as complete descriptions. In addition there are notes regarding the habitat, range, and, when known, the chromosome number is also given. The authors state that the descriptions have been drawn up "afresh" from living material or herbarium specimens. The keys, whenever possible, make use of characters at least as easy to observe in the field as in the herbarium.

The arrangement of the families follows, in general, that of Bentham and Hooker, although a number of alterations are made in an attempt to bring it in line with more modern ideas. Those accustomed to the older British floras will find a number of unfamiliar names. Many of these have been necessitated by the application of the principle of priority which has always been a firm feature of the International Rules of Botanical Nomenclature. Dr. Tansley, in the foreword, expresses himself in favor of the principle of *nomina conservanda* as applied to specific epithets. Such a procedure would be, however, fraught with difficulties and is not favored by the majority of botanists as is attested to by the fact that it has always been soundly defeated whenever the question has been presented for discussion at an International Botanical Congress.

In the preface we are informed that a volume of illustrations is being prepared but will probably not be completed for some time. *John R. Reeder.*

Écologie (Colloques Internationaux du Centre National de la Recherche Scientifique, XXXIII). 1952. 348 pp., paper bound. Service des Publications, Centre National de la Recherche Scientifique; 45, Rue d'Ulm; Paris-V°, France. 2700 francs. Papers presented at the International Ecology Colloquium in Paris in 1950 (see *Ecology* **31**: 478) were first published as fascicles 2, 4, 6, and 7 of volume 27 of *Année Biologique.* They have now been reissued as a single volume with separate pagination. The 38 contributions are written in French and English. Most of them deal with a wide variety of marine, fresh-water, and terrestrial animal ecology, and a smaller number are concerned with problems of general ecology. This book should be especially useful as a supplement, since many of the papers deal with fundamental aspects of ecology that are ignored or treated only superficially in textbooks. *R. W. Pennak.*

Hartman, C. G., and others. 1952. *World population problems and birth control.* Ann. N. Y. Acad. Sci., **54** (5): 729–868. $3. This symposium represents the views of twenty scientists in divers fields on the "population problem," which is to say the overpopulation problem. Fourteen papers are included, along with summaries of discussion by the participants. The reality of the problem is admitted by all, but the participation of a number of clinicians, extremely valuable though it is, has had the unfortunate result of creating a dichotomy that somewhat mars the total effect. This is because the medical men have an eminently practical approach to the small fraction of the problem that concerns them. The causes of human fertility and infertility are reasonably well understood, and particularly ingenious and enlightening accounts of events in male and female genital tracts before, during, and after coitus are contributed by W. T. Pommerenke, M. A. Breckenridge, and John MacLeod. New developments in contraceptive technique are discussed by several others with equally scientific precision. The sociologists and cultural anthropologists, on the other hand, despite a good deal of thought, have been able to bring little to the symposium beyond a worried attitude, soundly backed by statistics. Birth control by overproductive people is the obvious answer to the overpopulation problem, but we seem to be no nearer to knowing how to get them to apply it than we were before the symposium was held. At any rate, this collection of papers is thoughtful, broadly based, and should "awaken interest," which was its chief objective. Copies may be obtained from the New York Academy of Sciences, 2 East 63rd St., New York 21, N. Y. *E. S. Deevey.*

Henbest, L. G., and others. 1952. *Distribution of evolutionary explosions in geologic time.* Journ. Paleontol., **26** (3): 298–394. $2. A symposium sponsored by the Paleontological Society, the Society of Vertebrate Paleontologists, and the Geological Society of America,

this volume contains seven major papers by eight authors and discussion by eleven others. It presents an admirable summary of present knowledge of evolutionary rates in a variety of organisms, and thus forms an exceedingly useful companion-work to G. G. Simpson's "Tempo and Mode in Evolution." Its focus, however, is not on evolutionary rates as such, but on the doctrines held about them, often unconsciously, by some geologists. The geologic record has numerous gaps and contains undoubted episodes of almost world-wide mountain building. The view that these episodes have had a characteristic rhythm has carried over into stratigraphic practice, so that some paleontologists believe that the organic record is also pulsatory, with waves of evolution and extinction succeeding each other in synchrony with crustal movements. To a large extent this is a false impression arising from failure to appreciate the importance of gaps in the stratigraphic record, and is bolstered by circular reasoning, as when mammalian faunas lacking dinosaurs are dated as post-Mesozoic because the dinosaurs died out with the Laramide revolution. The chief merit of this symposium is to expose such fallacies. Evolutionary rates seem to have fallen into patterns during geologic time, as discussed particularly in Simpson's paper on vertebrates and in N. D. Newell's on invertebrates, and while the meaning of these patterns is not altogether clear, it is obvious that diastrophism has had little or no systematic influence on them. The symposium is a major contribution to evolutionary (and ecologic) literature; copies may be obtained from the Secretary of the Paleontological Society. Dr. Kenneth E. Caster, University of Cincinnati, Cincinnati 21, Ohio. *E. S. Deevey.*

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